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CAUSES OF VARIATION IN PREY PROFITABILITY AND ITS CONSEQUENCES FOR THE INTAKE RATE OF THE OYSTERCATCHER *HAEMATOPUS OSTRALEGUS*

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Prey species have different morphological and behavioural adaptations to escape their predators. In this paper we review how these prey defenses affect prey profitability and intake rate for one predator, the Oystercatcher. Four rules govern profitability. First, within each species large prey are more profitable than small prey, because flesh content increases more steeply with prey size than handling time. Second, soft-bodied prey, such as worms and leatherjackets, which can be swallowed whole, are much more profitable than armoured prey, such as bivalves, which Oystercatchers have to open before the flesh can be extracted from the shell. Third, heavily armoured surface-dwelling prey, like Mussels and Cockles, are the least profitable prey of all, even if the armour is bypassed through stabbing the bill between the valves. Fourth, within the burying prey species, the profitability of prey decreases with depth. Hence burying bivalve species that bury in winter at larger depth than in summer, are in winter, if not out of reach of the bill, anyway less profitable.

Despite the large differences between the profitabilities of the various prey species, the intake rates do not differ much when the prey species are compared, presumably because prey with a low profitability are only exploited if the search time is relatively short, i.e. if the density of harvestable prey is high. On the other hand, within each species, the intake rate goes up if larger, more profitable prey are taken. Thus, if the birds have to feed on smaller prey specimens, they fail to fully compensate for the low profitability by an increase in the rate at which these prey are found. Although the profitability of prey differs seasonally due to the variation in the prey condition, only a small seasonal variation in the intake rate was found. Because burying bivalves and soft-bodied worms bury deeper and are less active in winter, Oystercatchers necessarily rely on bivalves living at, or just beneath, the surface at that time of year.

Key words: Oystercatcher - *Haematopus ostralegus* - optimal diet model - prey profitabilty - food intake rate

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INTRODUCTION

Oystercatchers *Haematopus ostralegus* feed on at least 15 different prey species along the NW. European coast (Cramp & Simmons 1983, Hulscher 1996). On intertidal sand and mudflats, their food consists of Cockles *Cerastoderma edule* and Mussels *Mytilus edulis*, and to a lesser degree also of other bivalves, such as *Macoma balthica*, *Scrobicularia plana* and *Mya arenaria*, worm species, such as *Arenicola marina* and *Nereis diversicolor*, and the Shore Crab *Carcinus maenas*. On rocky shores, Oystercatchers take limpets *Patella aspara* and *P. vulgata*, Periwinkles *Littorina littorea* and Dogwelks *Nucella lapillus*, whereas in grassland they select mainly different earthworm species (Lumbricidae) and leatherjackets (larvae of the crane fly *Tipula paludosa*).

Except for the worms and leatherjackets, all species selected by Oystercatchers are armoured with a calcified exoskeleton. Nonetheless, Oystercatchers never swallow the hard skeletal parts. Instead, they eat the flesh from bivalves, snails or crabs after prizing, or stabbing, the bill between the valves or hammering a hole in the shell or carapace. Oystercatchers may easily find prey lying at the surface but they have to spend time breaking in and extracting the flesh. It takes more time for an Oystercatcher to locate benthic bivalves living hidden in the substrate, since these prey are usually found by randomly probing the bill into the mud (Hulscher 1976, 1982, Wanink & Zwarts 1985). Moreover, since these buried prey are also armoured against predation, Oystercatchers must, as with surface prey, spend time in opening them. In contrast, soft-bodied prey are ready to eat. They are also buried and must be searched for, but they are an easy prey for Oystercatchers when they come to the surface to feed themselves (Ragworms *Nereis*) or to defecate (Lugworms *Arenicola*).

The extent to which various prey species provide a staple food for the Oystercatcher varies dramatically with season. Inland fields are heavily exploited by breeding birds in spring and summer, but only used as a supplemental food resource by most Oystercatchers in winter (Heppleston 1971, Daan & Koene 1981, Goss-Custard & Durell 1984). On the tidal flats, *Macoma* is taken in early spring, whereas *Nereis* predominates in late spring (Bunskoeke *et al.* 1996). Both prey are only locally important. In contrast, as the papers reviewed below show, Mussels and Cockles are universally important winter foods. The fact that Shore Crabs are only taken in summer is easily explained by their migration to deeper water in autumn (e.g. Beukema 1991). However, the other prey occur year-round in the same habitat, with many individuals growing for several years. We take as a working hypothesis that the seasonal changes in the utilization of these prey by the Oystercatcher population are primarily due to seasonal changes in harvestability of the prey, i.e. the prey fraction that is both accessible and profitable (Zwarts & Blomert 1992, Zwarts & Wanink 1993). By definition, harvestability is negatively related to the effectiveness of the morphological and behavioural anti-predator defenses of the prey. Since each prey species has different adaptations to reduce predation risk, we may also expect differences between prey species in the time of year when the defenses are most effective.

The intake rate is defined as mg s^{-1} feeding, thus the quotient of weight of the prey and feeding time. Feeding time consists of two components: searching and prey handling. Hence the intake rate is the product of two ratios:

prey weight/handling time × *handling time/* (*search* + *handling time*).

The first ratio, the intake rate during prey handling, is called the profitability. The second ratio is the relative handling time, the proportion of the feeding time during which the bird handles the prey.

It is obvious that the intake rate will increase when the prey are large, are handled in a short time, and/or when the search time between prey is limited. Several studies (Hulscher 1976, 1982, Wanink & Zwarts 1985, Habekotté 1987, Goss-Custard *et al.* 1996b) show that search time of Oyster-

catchers decreases as prey density increases. Several others support the corollary that the rate at which prey are taken increases with prey density (Goss-Custard 1977, Sutherland 1982b, Triplet 1990, Ens *et al.* 1996c). Most of these positive results were obtained on Oystercatchers feeding on Cockles which, due to their shallow depth, are always within reach and detectable by touch. In contrast, the depth distribution of burying bivalves differs seasonally and locally (Zwarts & Wanink 1993) and this, as will be discussed, affects the profitability and the intake rate. Due to variation in the thickness of the shell, the degree to which barnacles cover Mussels, and several other variables (Goss-Custard *et al.* 1996b), the fraction of harvestable Mussels is even more variable and very hard to assess.

To understand the variation in intake rate it is not sufficient to measure the relationship between intake rate and prey density. This paper focuses on the dependence of intake rate on prey profitability. One of the main conclusions of this paper is that, within each prey species, the weight of the prey greatly affects the profitability and thereby the intake rate. To investigate to what degree prey profitability and intake rate differ between surface and buried prey, and between hard-shelled and soft-bodied prey, we review all available Oystercatcher studies on prey profitability and intake rate. First, we explore whether, within a species, the handling time depends not only on prey size, but also on prey condition, i.e. the relative deviation from the average weight per size. The next step is to relate handling time and prey profitability to prey weight and to examine whether prey species differ in the time Oystercatchers need to eat a given amount of flesh. The paper analyses the feeding time per prey (i.e. searching + handling time) as a function of prey weight separately for the species and for all species taken together. Since the prey condition varies seasonally, we also test whether this affects intake rate. The companion paper (Zwarts *et al.* 1996d) will investigate whether the described relationships of prey profitability and intake rate as a function of prey size and prey weight can be used to predict in detail the decision of Oystercatchers to take only certain prey from a mixture of different size classes and prey species.

METHODS

Studies

The data presented in this paper have been taken from 57 articles, six student reports, four unpublished theses, but also from unpublished data files of Anne-Marie Blomert, Klaus-Michael Exo, Kees Hulsman, Cor Smit and the five authors; all sources are listed in the appendix. The studies were performed in 20 areas (Fig. 1), of which ten are situated in Great Britain and Northern Ireland, six in the Netherlands and one in Denmark, France, Morocco and Mauritania. All studies were done in the field on free-living Oystercatchers, except those indicated as C in column 'Cap' of the appendix which refer to caged birds. Captive birds were either taken to the mudflats where they were allowed to feed in temporary cages (Hulscher 1976, 1982, unpubl.) or they were offered food on artificial mudflats (e.g. Swennen *et al.* 1989). Captive birds thus fed in an almost natural situation, but occasionally the food supply was manipulated either by erasing surface tracks that might reveal the presence of the prey (Hulscher 1982), or by implanting prey at different depths (Wanink & Zwarts 1985, 1996).

Prey size

Size classes taken were known because prey remnants could be collected, and/or the prey size was estimated when the birds held the prey in the bill. In the latter case, bill length or the size of the colour ring could be used as a ruler of known size. Calibration experiments showed that observers could estimate prey size this way rather consistently (Ens 1982, Blomert *et al.* 1983, Goss-Custard *et al.* 1987, Boates & Goss-Custard 1989, Ens *et al.* 1996b). Such estimates were usually accurate. In others, errors could be corrected. For instance, comparison of the size frequency distribution of remnants of fiddler crabs *Uca tangeri* ta-

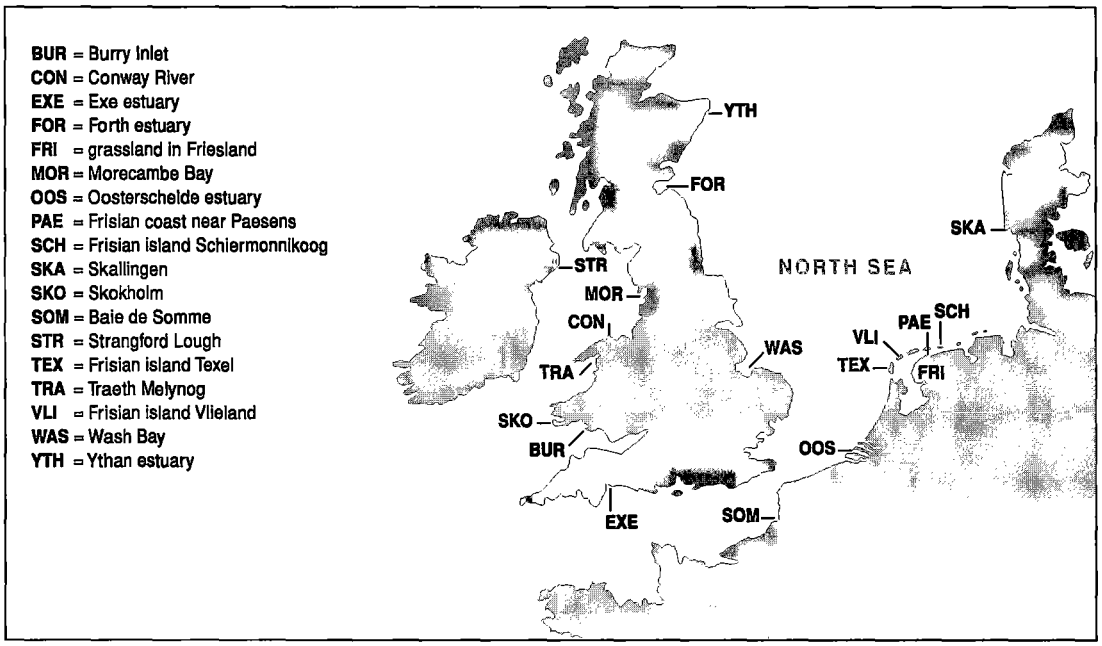

Fig. 1. Map of the study areas in NW. Europe indicated by three letter codes. Two study areas were situated in Africa: the Bay of Dakhla, Morocco (formerly Western Sahara) and the Banc d'Arguin, Mauritania.

ken by Oystercatchers (Ens unpubl.) and size of estimates of *Uca* obtained visually, as they were being taken (Ens *et al.* 1993), showed that the visual estimates were systematically 5 mm too low.

Since Oystercatchers only ingest soft flesh, faecal analysis did not reveal information on prey size selection. However, if Oystercatchers swallowed the prey whole, hard prey fragments found in the excreta could be used to predict the prey size taken, as shown by Durell *et al.* (1996), who measured the jaws of Ragworms, and Zwarts & Blomert (1996) who did the same for jaws and head capsules of leatherjackets.

Prey weight

Although the best measure of prey value would be assimilated energy, we have to rely on gross intake of biomass for two reasons. First, except for a few studies (Speakman 1984, Kersten & Visser 1996 and Zwarts & Blomert 1996), the digestibility of the natural food of Oystercatchers has not yet been measured. However, since the biochemical composition of the flesh of marine bivalves does not vary much (e.g. Dare & Edwards 1975, Beukema & de Bruin 1979), we assume also that the digestibility of this type of food for Oystercatchers does not vary much either and will remain close to 85%, such as found by Speakman (1984) and Kersten & Visser (1996) for mussel flesh. Second, too few studies have measured the caloric content of the food taken by Oystercatchers. However, the available studies (e.g. Brey *et al.* 1988, Dauvin & Joncourt 1989, Zwarts & Wanink 1993) suggest that the variation is not large, usually between 22 and 23 kJ g^{-1} ash-free dry weight (AFDW). Hence we take the rate of AFDW consumption as a general measure of prey profitability and intake rate.

Dare (1975) found a weight loss of 12.8% if Mussels were stored in formalin. Corrections for weight loss due to formalin have been made in the studies of Meire & Ervynck (1986), Meire (1996b) and Exo *et al.* (unpubl.); these studies are indicated with F in column 'Lab' of the appendix. The

first quantitative studies in the fifties and sixties expressed food consumption not in terms of AFDW, but as volume, wet weight or dry weight. Column 'Lab' in the appendix indicates which studies give intake rate as volume (V), wet weight (W) or dry weight (D). Volume (ml) of flesh, determined by emersion in water, is equivalent to 90-93% of its wet weight (mg) (Drinnan 1958b, Hulscher 1982). The dry weight of bivalve flesh is 15% to 20% of the wet, or fresh, weight (Hulscher 1974, 1982, Kersten & Visser 1996). The variation in this ratio depends on the laboratory procedures used. The water content varies between 79 and 82% if the flesh is briefly patted dry, but is some percentage points lower if it remains longer on a filter paper and higher if water on the surface of the flesh is not removed (Zwarts unpubl.).

Dry weight includes inorganic material. The ash-free dry weight (AFDW) of the flesh of marine invertebrates varies between 75 and 90% of the dry weight. A part of this variation may be attributed to the season (Zwarts 1991), but the main source of variation is again the laboratory procedure. The ash content of the flesh drops to 10-15% if the animals have been stored in clean sea water, but if their alimentary tract is still full of sediment, the ash percentage can be as high as 25 or even 30%. For estuarine prey species, we take a common conversion factor of 0.16 to estimate AFDW if only wet weight is known and 0.17 if only volume has been determined. If the AFDW of prey has not been measured but derived from the volume or wet weight by using these conversion factors, the error of the estimate may be as much as 25% due to variation in the water content of the prey and, especially, the variable amount of ash. The error is still larger in earthworms in which the ash content varies between 25 and 55%.

The relationship between size and weight of the prey has been determined in all studies. If a paper did not give the average prey weight, we calculated it from the frequency distribution of the size classes taken and the size-weight relationship. In a few studies, the frequency distribution was not given. In those cases the weight of the average length class was taken as the average weight. This underestimates, inevitably, the average prey weight, especially if the range of size classes taken was large due to the exponential increase of weight with size.

Some prey were incompletely consumed and additional data have to be collected to know how much flesh remained in the shell (Zwarts & Wanink 1984, Swennen 1990). For instance, Oystercatchers feeding on fiddler crabs (Ens *et al.* 1993), opened the carapace and took the flesh piecemeal but refused the pincers and legs, hence ignoring half of the biomass of the large specimens (Zwarts & Dirksen 1990). A more difficult error of estimate arose if prey were stolen as they were being eaten, or when Oystercatchers leave behind considerable amounts of flesh in the prey, which were subsequently consumed by other waders. This makes it hard to estimate the fraction of the prey biomass that was actually taken, a problem faced by Swennen (1990) in quantifying the intake rate of birds feeding on Giant Bloody Cockles *Anadara senilis*.

These problems did not arise when the weight of the flesh taken was not derived indirectly from the prey size but instead from direct estimates of the amount of flesh swallowed. The size of pieces of flesh extracted from the prey was estimated and converted to prey weight using calibration experiments with model Oystercatchers in which observers estimated the size of morsels of flesh held near the bill (Blomert *et al.* 1983, Goss-Custard *et al.* 1987, Kersten & Brenninkmeijer 1995, Ens & Alting 1996b). This alternative way of estimating prey weight is the only one that can be used if the size of the individual prey was unknown as, for instance, when the flesh was extracted from prey opened beneath the surface.

Profitability

Profitability is defined as mg AFDW per second prey handling. Unless stated to the contrary, this only refers to prey which are actually consumed. Profitability can also be calculated taking into account the time lost on prey that were handled but not taken. The time spent in handling

prey taken, and not taken, is known as the 'positive' and 'negative' handling times, respectively. To include negative handling times in the calculation of the profitability, it is necessary to known how often prey of a given size class are not taken and how much time is lost each time. Usually, the inclusion of lost handling times does not matter much, since either the negative handling times are very short, and/or very few prey are rejected, as shown for Ragworms and *Macoma* by Ens *et al.* (1996a). Important exceptions are Mussels being hammered on the dorsal, and especially on the ventral side (Meire & Ervynck 1986, Cayford & Goss-Custard 1990). The feeding method used when eating Mussels is indicated in column 'Mus' of the appendix.

Intake rate

Intake rate is defined as mg AFDW consumed per second of feeding. Feeding time excludes preening and resting pauses, but includes short bouts of aggressive behaviour. Most data are based on observation periods of 5, 10 or 15 minutes. In some cases, however, individual birds were watched continuously for the entire low water period (Blomert *et al.* 1983, Ens & Goss-Custard 1984), or both methods were used (Ens *et al.* 1996b).

Some studies concerned Oystercatchers taking a mixture of prey species. In these cases, observation periods were selected during which at least 80% (and occasionally 100%) of the ingested biomass belonged to one species. This may cause errors of estimation. If an Oystercatcher generally feeds only on a small prey and only incidentally takes a large one, 5 min periods during which only the large species are taken tend to give untypically high intake rates which birds may seldom attain were they to feed solely on these prey. This was presumably the case in Oystercatchers taking large *Mya* or *Arenicola* while their main prey, *Macoma* and *Nereis*, were smaller (Bunskoeke 1988). According to the same reasoning, estimates of intake rate of small prey taken from feeding bouts with large prey may be spuriously low.

We will investigate the relationship between intake rate and the prey density for Oystercatchers feeding on *Cerastoderma*, but not in the other prey species; see Goss-Custard *et al.* (1996b) for mussel-eating Oystercatchers. Column 'nm^{-2}' in the appendix gives the cockle densities.

Available feeding period

The maximal duration of the feeding period in tidal areas is determined by the exposure time of the feeding area which is usually situated at, and below, mean sea level. The main feeding areas of Oystercatchers, cockle and mussel beds, are available for 5-6 h over an average low water period. The exposure time would overestimate the duration of the feeding time for breeding birds, since they visit the low water feeding areas only in short bouts (e.g. Ens *et al.* 1996b). These measurements are marked with a B in the column 'Br'. The available, sometimes extremely short, feeding periods in captive birds were varied experimentally. Column 'Time' in the appendix gives the duration of the feeding period.

Feeding activity

The feeding activity was determined in two ways. Counts of feeding and non-feeding birds were conducted at regular intervals over the entire low water period. The alternative was to measure continuously the non-feeding time in individual birds of which the feeding behaviour was registered over long periods. Column 'Feed' in the appendix gives the percentage of the time actually spent feeding.

Consumption

The product of intake rate, duration of the feeding period and the percentage of time spent feeding, estimates the total consumption during the feeding period, given in column 'Cons' of the appendix. The feeding period refers to the total daylight period in non-tidal habitats and to the low water period by day in tidal habitats. The appendix gives in column 'Cons' the available estimates of consumption.

Analysis

We assembled two data files from the literature and our own unpublished data. One contained measurements of the handling time by prey species and by prey size and/or prey weight. The other contained the intake rates of Oystercatchers feeding on a single prey species. If studies spanned several months or years, the data were subdivided by month if intake rates were available for each month and based on sufficient measurements and prey weight and intake rate differed between the months. The same criteria were used to decide whether data would be given separately or lumped for different study plots within the study area or for different individual birds being studied. The intake rates were lumped in the few cases that the intake rates were known per Oystercatcher age class. Since the paper investigates the effect of prey density on intake rate in *Cerastoderma*, the intake rates from four studies have been split up for different subareas where prey size, prey density and intake rate were measured. SPSS (Norušis 1990) was used for all statistical analyses.

RESULTS

Handling time of armoured prey in relation to prey size, opening technique and burying depth

The smallest armoured prey opened by Oystercatchers were spat Cockles 8 mm long with an AFDW of 3.3 mg (Meire 1996b). The largest prey taken were Giant Bloody Cockles *Anadara* which is the food supply of Oystercatchers wintering on the Banc d'Arguin, Mauritania (Swennen 1990). These birds ate prey that were, on average, 78 mm long containing 3300 mg AFDW. Even larger prey were taken by Oystercatchers in captivity, as well as in the field, when offered large *Mya* 88 mm long with a flesh content of 4200 mg AFDW. However, since these prey usually lie out of reach of the bill (Zwarts & Wanink 1984), they cannot

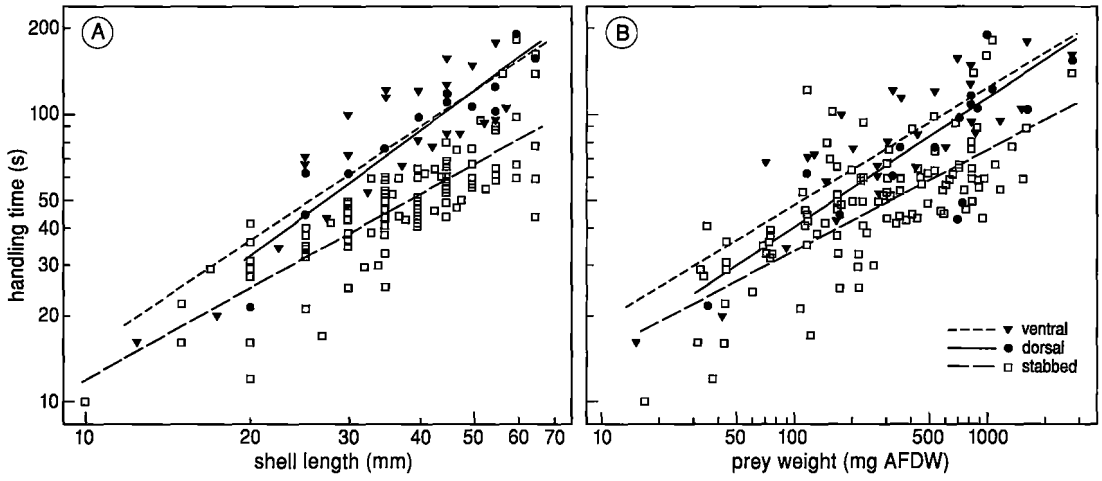

Fig. 2. Handling time as a function of (A) prey length or (B) prey weight in *Mytilus* opened by Oystercatchers stabbing the bill between the valves or hammering the shell on the dorsal or ventral side. Sources: Koene (1978), Zwarts & Drent (1981), Ens (1982), Blomert *et al.* (1983), Speakman (1984), Linders (1985), Meire & Ervynck (1986), Sutherland & Ens (1987), Cayford & Goss-Custard (1990), Ens *et al.* (1996b), Hulscher (unpubl.). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other according to covariance analyses: $R^2 = 0.593$ for prey length and $R^2 = 0.168$ for the three techniques (left); $R^2 = 0.620$ for prey weight and $R^2 = 0.100$ for the three techniques (right).

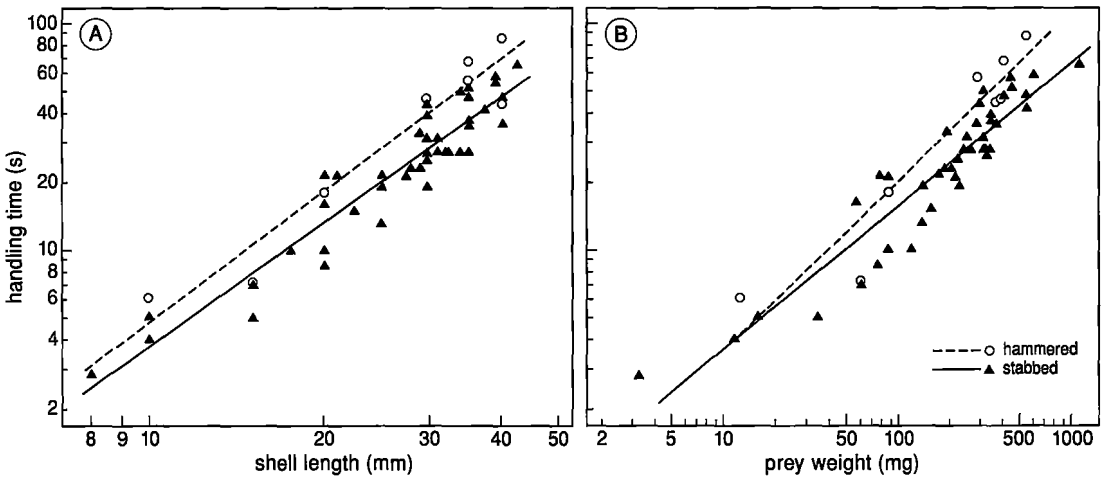

Fig. 3. Handling time as a function of (A) prey length or (B) prey weight in *Cerastoderma*, given separately for Oystercatchers opening Cockles by stabbing the bill between the valves or hammering the shell. Sources: Hulscher (1976 & unpubl.), Sutherland (1982c), Swennen *et al.* (1989), Triplet (1994a), Ens *et al.* (1996b & c). The two regression lines (see also Table 1) differ significantly ($p = 0.002$) from each other according to covariance analyses: (A) $R^2 = 0.875$ for prey length and $R^2 = 0.024$ for both techniques; (B) $R^2 = 0.868$ for prey weight and $R^2 = 0.016$ for both techniques.

be considered as normal prey for Oystercatchers. Cockle spat could be handled in some seconds, but it took an Oystercatcher 212 s and 265 s, on average, to consume the flesh from the large *Anadara* and *Mya*. Thus, the handling time increases with flesh weight, as is further analysed in this section.

Although prey size explained a substantial part of the variation in handling time, there remained a large residual variation within each size class. In Mussels, a large part of this variation could be attributed to the technique used to open the Mussel (Fig. 2). Oystercatchers using the stabbing technique took less time than those which hammered Mussels on the dorsal side of the shell. The handling times were especially long when Mussels were torn off the bed, turned upside down and hammered on the ventral side (Cayford & Goss-Custard 1990, Fig. 2). Cockles were usually opened by stabbing, or forcing, the bill between the valves, but sometimes by hammering the shell. Ens *et al.* (1996b) found that it took Oystercatchers more time to open Cockles by hammering than by stabbing, just as in Mussels (Fig. 3).

The handling time also increased with shell length and flesh weight in *Scrobicularia* but it also depended on the depth at which the prey lived beneath the surface (Fig. 4). Wanink & Zwarts (1985) found that the time needed to handle *Scrobicularia* 37 mm long increased from 18 to 42 s as the burying depth increased from 0 and 5 cm (Fig. 4). Wanink & Zwarts (1996) offered Oystercatchers prey of different size but buried at a depth of 2 cm beneath the mud surface. All size classes were handled rapidly. The handling time of *Scrobicularia* of different size has also been measured in the field, but no attempts have been made to estimate the depth from which the prey are extracted. It is obvious, however, that most prey in winter were taken after the bill had been inserted fully into the substrate, whereas in summer the majority were taken from nearer the surface. Such a difference was to be expected, since most *Scrobicularia* in winter live out of reach of the Oystercatcher's bill (Zwarts & Wanink 1991,

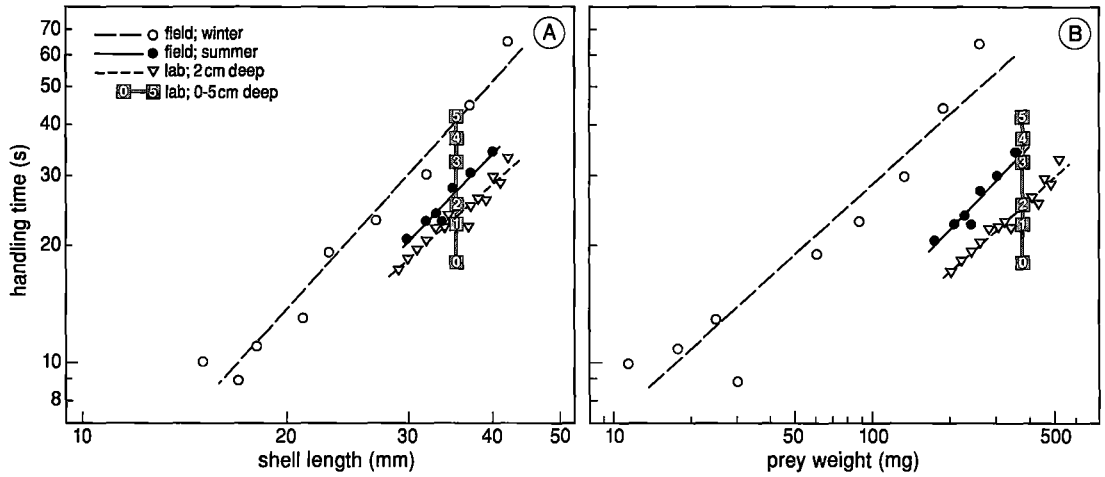

Fig. 4. Handling time as a function of (A) prey length or (B) prey weight in *Scrobicularia*, given separately for field data collected in winter (Habekotté 1987, Boates & Goss-Custard 1989), or in summer (Blomert *et al.* 1983) and for captive birds offered prey of similar size at different depths (Wanink & Zwarts 1985) or for different size classes buried to the same depth of 2 cm (Wanink & Zwarts 1996). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other, according to covariance analyses: (A) $R^2 = 0.848$ for prey length and $R^2 = 0.089$ for the three groups; (B) $R^2 = 0.674$ for prey weight and $R^2 = 0.219$ for the three groups.

1993); probably, all prey taken are only just accessible at a depth of 6 cm or 7 cm beneath the surface. In contrast, *Scrobicularia* live at shallower depths in summer, and some prey may be found at a burying depth of just a few centimeters only. In winter it took 1.4 times more time as in summer to handle *Scrobicularia* of similar size (Fig. 4). We conclude that the longer handling times in winter were entirely due to the greater burying depth of the prey.

The handling times of *Macoma* also increased with size (Fig. 5). It also seems likely that, just as in *Scrobicularia*, handling time increased with prey depth. *Macoma* live in the upper three cm of the substrate from April through July, increase their depth from August onwards and live about twice as deep in winter as in summer (Reading & McGrorty 1978, Zwarts & Wanink 1993). No studies were available for Oystercatchers feeding on *Macoma* in autumn and winter, probably because they are not taken then. However, within the summer half of the year, handling time varied seasonally, being in August 1.5 times as long as in spring and early summer (Fig. 5A); this is presumably due to the greater depth from which the prey were obtained in August. This comparison refers to field studies in which prey were lifted to the surface. However, *Macoma* are also eaten *in situ*, and in this case handling times are much shorter (Fig. 5A & B). Captive Oystercatchers lifted deep-living prey more often than shallow prey (Wanink & Zwarts 1985, Hulscher *et al.* 1996), so we assume that prey were eaten more often *in situ* during summer, whereas in early spring and late summer when they live at greater depth they were more lifted. Bunskoeke *et al.* (1996) provided some tentative support for this idea from free-living birds. As a consequence, the combined handling time of *Macoma* being lifted and eaten *in situ* will be short when the prey live close to the surface from April to July, the difference between late summer and early spring being perhaps twofold.

There is no variation in the burying depth of *Mya* during the year, so we expected no seasonal, prey depth-related variation in the handling time, as found in *Scrobicularia* and in *Macoma*. All the handling times in Fig. 6A were obtained in the la-

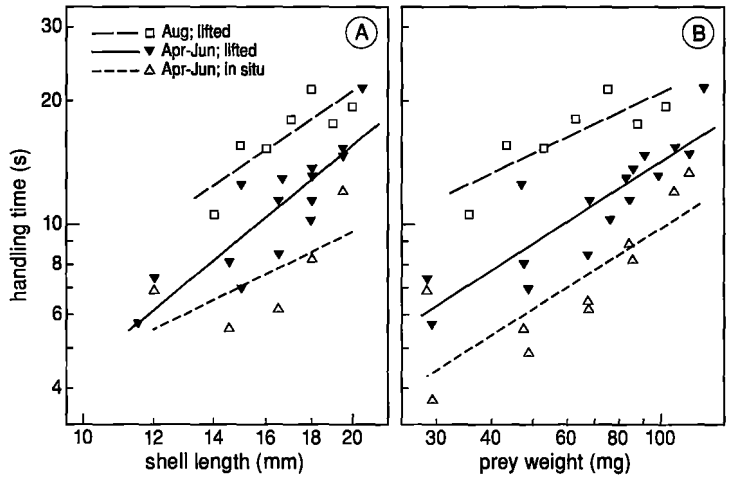

Fig. 5. Handling time as a function of (A) prey length or (B) prey weight in *Macoma*, given separately for prey eaten *in situ* or lifted to the surface and eaten there; the latter is divided into two periods (April-June, August). Sources: Hulscher (1982 & unpubl.), Blomert *et al.* (1983), Ens *et al.* (1996a), Hulscher *et al.* (1996). The three regression lines (see also Table 1) differ significantly ($p < 0.001$) from each other according to covariance analyses: (A) $R^2 = 0.490$ for prey length and $R^2 = 0.326$ for the three groups: (B) $R^2 = 0.402$ for prey weight and $R^2 = 0.445$ for the three groups.

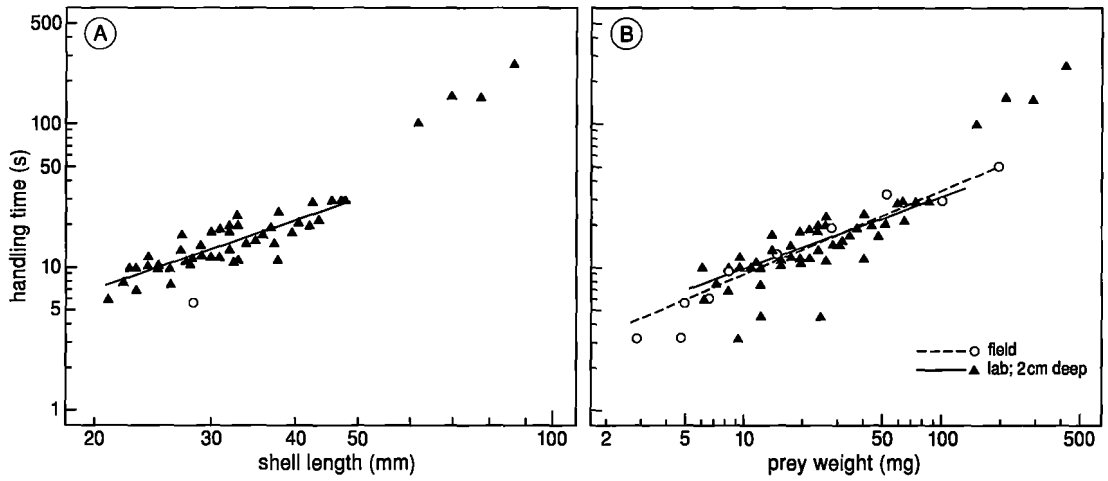

Fig. 6. Handling time as a function of (A) prey length or (B) prey weight in *Mya* in captive Oystercatchers feeding on prey lying at a depth of 2 cm (Wanink & Zwarts 1996) or wild birds feeding on clams from which the flesh is eaten *in situ* (Zwarts & Wanink 1984, Bunskoeke *et al.* 1996 & unpubl.). The regressions are calculated without the four largest clams since their handling times were untypically long. The handling times as a function of prey weight are not significantly different for the two groups ($p = 0.33$ in panel B). Results of covariance analyses: (A) $R^2 = 0.853$ for prey length; (B) $R^2 = 0.869$ for prey weight and $R^2 = 0.002$ for the two groups; Table 1 gives more details.

Table 1. Handling time as an exponential function of length (L, mm) or weight (W, mg) of the prey. The last column gives the number of the figure where the regression lines are depicted.

Species	Category	Regression	R	n	Fig.
Mytilus	ventral	$0.712L^{1.313}$	0.86	26	2A
Mytilus	dorsal	$0.443L^{1.432}$	0.93	14	2A
Mytilus	stabbed	$0.975L^{1.081}$	0.82	99	2A
Cerastoderma	hammered	$0.054L^{1.945}$	0.96	8	3A
Cerastoderma	stabbed	$0.053L^{1.846}$	0.95	42	3A
Scrobicularia	field; winter	$0.046L^{1.905}$	0.98	9	4A
Scrobicularia	field; summer	$0.041L^{1.823}$	0.96	7	4A
Scrobicularia	lab; 2 cm deep	$0.093L^{1.549}$	0.98	14	4A
Macoma	Aug; lifted	$0.262L^{1.466}$	0.83	7	5A
Macoma	Apr-Jun; lifted	$0.076L^{1.778}$	0.87	16	5A
Macoma	Apr-Jun: *in situ*	$0.408L^{1.055}$	0.67	5	5A
Mya	lab; 2 cm deep	$0.070L^{1.546}$	0.80	44	6A
Mytilus	ventral	$7.258W^{0.411}$	0.84	26	2B
Mytilus	dorsal	$5.114W^{0.451}$	0.92	14	2B
Mytilus	stabbed	$6.549W^{0.355}$	0.78	99	2B
Cerastoderma	hammered	$0.625W^{0.750}$	0.95	8	3B
Cerastoderma	stabbed	$0.817W^{0.637}$	0.93	42	3B
Scrobicularia	field; winter	$1.821W^{0.598}$	0.95	9	4B
Scrobicularia	field; summer	$0.541W^{0.701}$	0.96	7	4B
Scrobicularia	lab; 2 cm deep	$0.675W^{0.610}$	0.98	14	4B
Macoma	Aug; lifted	$2.212W^{0.487}$	0.83	7	5B
Macoma	Apr-Jun; lifted	$0.694W^{0.655}$	0.87	16	5B
Macoma	Apr-Jun; *in situ*	$0.508W^{0.642}$	0.83	10	5B
Mya	combined	$0.661W^{0.586}$	0.91	54	6B
Nereis		$0.378W^{0.481}$	0.96	35	7
Arenicola		$0.387W^{0.539}$	0.98	7	7
Earthworms		$1.489W^{0.216}$	0.52	10	7

boratory, except for those obtained in one field study. Figure 6A shows the handling time of clams up to 90 mm long. Free-living Oystercatchers rarely find *Mya* larger than 40 mm long, since these large clams live out of reach of the bill (Zwarts & Wanink 1984, 1989, 1993). All clams in the laboratory experiments were buried, however, at a depth of about 2 cm and so at an extremely shallow depth compared to the natural situation, at least for the larger size classes. This means that, as in *Scrobicularia*, the handling times of the larger size classes would be about twice as long if the prey were taken from a depth of 5 or 6 cm, as would be usual in the field. The single field study found that, in contrast to the expectation, Oystercatchers handled the prey in less time than in the laboratory (Fig. 6A). However, while the Oystercatchers in the laboratory ingested all the flesh from the shell, the birds in the field often only took the siphon and left behind the remaining part of the body (Zwarts & Wanink 1984). Another field study (Bunskoeke *et al.* 1996, pers. comm.) estimated the weight of the flesh extracted from *Mya* of unknown size, so more field data were available when handling time was plotted against the prey weight (Fig. 6B). As Fig. 6B shows, the relationship between handling time and prey weight was the same as in the laboratory, where all the flesh from shallow prey was eaten, and field studies, where a variable amount of flesh

was extracted from deep-living prey.

In conclusion, the handling time of all armoured prey species increases with prey size. An additional, and substantial, part of the variation in handling time may be explained by four other variables: (1) depth from which prey are taken; (2) whether prey are hammered or stabbed; (3) whether prey are opened *in situ* or opened after being pulled up from or off the sediment; and (4) portion of the prey eaten.

Handling time of bivalves in relation to prey condition

Figures 2-6 show the handling times as a function of prey length and of prey weight. If most of the handling time is spent in eating the flesh, we expect that the handling time would depend on the amount of flesh ingested and that the close relationship between handling time and prey size is due only to the high correlation between prey size and flesh weight. On the other hand, if handling time consists mainly of time spent in breaking the shell, handling time would be primarily determined by size-related strength of the shell and not by the amount of flesh ingested. Prey weight and prey size are so highly correlated, that it is hardly surprising that it is not possible to tell from Figs. 2-6 whether handling time depends on prey weight, and thus indirectly on size, or on prey size, and thus indirectly on the amount of flesh to be ingested.

Although flesh weight and prey size were highly correlated when both were plotted on a log-log scale, the weight variation within each size class was large enough to investigate whether the amount of flesh, independent of prey size, affected the handling time. Most of the species preyed upon by Oystercatchers contained in late winter 40% less flesh than specimens of similar size in early summer (Chambers & Milne 1979, Zwarts 1991, Zwarts & Wanink 1993, Ens *et al.* 1996b). Prey condition had been defined as percent deviation of the average prey weight, such as obtained by regressing log(*weight*) against log(*size*), using all data given in Figs. 2-6. Multiple regression analyses showed that handling time increased with prey length and that it also took, as expected, more time to handle Cockles and Mussels containing more flesh. These increases were not significant, however (Table 2). The relationships were even significantly negative in *Scrobicularia* and *Macoma*. The explanation is that in the latter two species prey condition and burying depth varied concurrently: they were meagre and buried deep in winter and had a good condition and were close to the surface in summer. As shown in the previous section, handling time increased with burying depth, so the negative correlation between handling time and prey condition was most likely due to the positive correlation between prey condition and burying depth (e.g. Zwarts 1991, Zwarts & Wanink 1993).

In conclusion, the increase of handling time with flesh content, such as shown by Ens *et al.* (1996b) for his data, is not found by us when data from different mussel and cockle studies were

Table 2. Handling time as a function of prey size and prey condition according to multiple regression analyses: a is the intercept, $b_1 \pm SE$ is the prey size (ln(*mm*)) and $b_2 \pm SE$ is the prey condition (ln(*per cent deviation from average weight for each mm class*)). The average weights are obtained by plotting for each species all weights against all sizes in Figs. 2-6. The analysis in *Mytilus* and *Cerastoderma* is limited to prey opened by stabbing. The prey condition has a non-significant, positive effect on the handling time in *Mytilus* and *Cerastoderma* and a significant, negative effect on the handling time of *Scrobicularia* and *Macoma*.

Species	a	b_1	SE	b_2	SE	R^2	n
Mytilus	-0.029	+1.081	0.075	+0.041	0.074	0.681	99
Cerastoderma	-2.950	+1.851	0.112	+0.273	0.200	0.945	36
Scrobicularia	-1.255	+1.254	0.157	- 0.572	0.155	0.582	61
Macoma	-2.452	+1.746	0.328	- 1.093	0.511	0.754	28

pooled. *Scrobicularia* and *Macoma* are even handled significantly more rapidly if they contain more flesh, but this is because body condition varies seasonally in accordance with burying depth.

Handling time of soft-bodied prey in relation to prey weight and burying depth

Figure 7 shows the relationship between handling time and prey weight in four soft-bodied prey: Ragworms, Lugworms, earthworms and leatherjackets. Handling time quadruples as prey weight increases thirtyfold. The handling times are short in these species for several reasons. First, no time was spent in opening, or preparing, the prey, since they were eaten whole. Moreover, soft-bodied prey were usually swallowed in one piece and not piecemeal. Further, most of these prey were picked up from, or taken from just beneath, the surface. Handling times were longer when the prey were extracted from the substrate. It took Oystercatchers, on average, 4 s to remove leatherjackets from their burrows, 2-4 cm deep, and only 1.3 s to mandibulate them (Blomert & Zwarts unpubl.). Hence, depending on the position of the leatherjacket in its burrow, the handling time varied between 2 and 6 s. We might expect an even larger difference in earthworms. When prey are found at, or just beneath, the surface, they can be grasped easily and transported up the bill in only one catch-and-throw movement (see Gerritsen 1988). But when prey are extracted from the turf, they often break and must therefore be eaten piecemeal. Whether the prey are at or beneath the surface presumably also explains the average differences in handling time between species. Lugworms, and the majority of the Ragworms, were grasped while they were close to the surface and at shallow depth in their burrows. In contrast, the leatherjackets and earthworms were, at least partly, extracted from the turf.

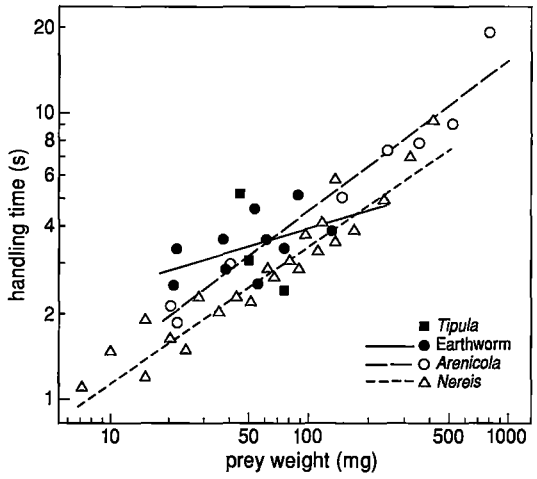

Fig. 7. Handling time as a function of prey weight (mg AFDW) in earthworms (Ens unpubl.), *Nereis* (Boates & Goss-Custard 1989, Ens *et al.* 1996a, Hulscher unpubl.), *Tipula* (Blomert & Zwarts unpubl., Ens unpubl.) and *Arenicola* (Bunskoeke 1988 & unpubl.). The handling times of the four species differ significantly according to a covariance analysis (R^2 = 0.918 for prey weight and R^2 = 0.025 for the species).

We conclude that soft-bodied prey are handled rapidly, unless they are extracted from the substrate. We assume that because Oystercatchers usually feed on estuarine worm species that appear at the surface, they are handled in less time than the grassland species which are more often extracted from the turf.

Profitability of armoured and soft-bodied prey

Figures 2-7 show the relation between handling time and prey weight in five armoured and four soft-bodied prey species. The profitability, the amount of flesh consumed per unit time handling, was calculated for these species, and also for *Anadara* and *Uca*, and plotted against their prey weight (Fig. 8). Worms and leatherjackets were, on average, 4.43 times more profitable than armoured prey of similar size. Although there was a large scatter in the profitability of the armoured prey, it is clear that the profitability of soft-bodied, as well as armoured prey, increases with prey weight.

The large scatter in the profitability of armoured prey could largely be explained by the species concerned and the technique used to open them. An analysis of covariance revealed that the eleven prey species alone explained 39.1 % of the

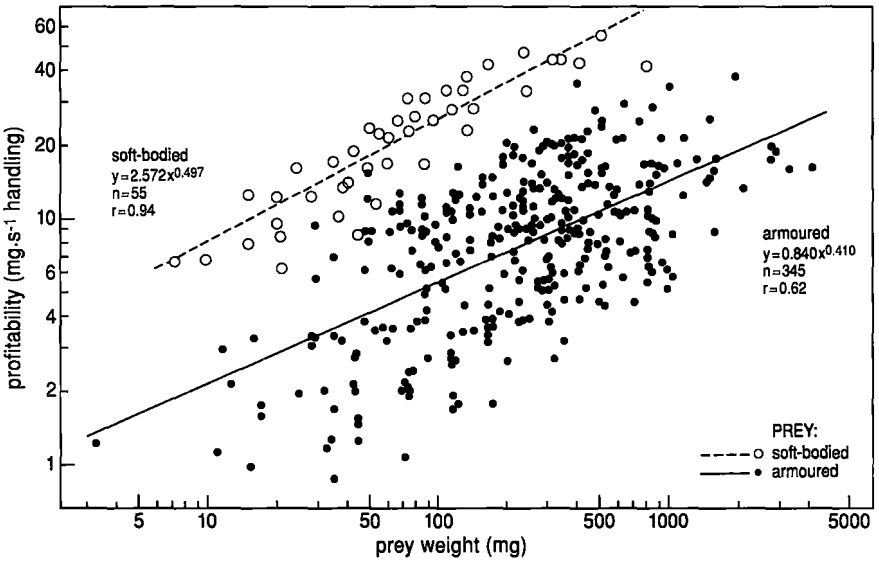

Fig. 8. Profitability (mg s^{-1} handling) as a function of prey weight (mg AFDW), given separately for soft-bodied prey (same data as Fig. 7) and armoured prey (in addition to the data given in Figs. 2-7, also *Anadara* (Swennen 1990), *Littorina* (Boates & Goss-Custard 1992), *Patella* (Safriel 1967) and *Uca* (Ens *et al.* 1993 & unpubl.). The regression lines are shown separately for soft-bodied and armoured prey. A multiple regression analysis revealed that non-parallel regression lines did not explain more variance than parallel ones (R^2 = 0.515 and 0.514, respectively). Hence a common exponent (0.421) may be used with different intercepts: 0.788 for armoured prey and 3.490 for soft-bodied prey.

variance, prey weight 15.1%, whereas 24.0% could be attributed to both. To visualize the differences in profitability between species, independently of prey weight, we regressed profitability against prey weight for the armoured and soft-bodied prey, without distinguishing among the species, and calculated for each species the average deviation from the regression line. Figure 9 is based upon these calculations and shows the average profitability per species, standardized to a prey weight of 200 mg. Four types of prey can be distinguished. First, soft-bodied prey taken from the surface had a profitability of 30-35 mg s^{-1}. Second, if soft-bodied prey were extracted from the substrate, their profitability was reduced to about half, as indicated for leatherjackets, but not shown as a separate category in Fig. 9. Third, the average profitability of bivalves living buried in the substrate was 10-15 mg s^{-1}, but was about half this value when prey had to be taken from a great depth. Fourth, hard-shelled prey found just beneath, or from the surface, were the least profitable (4-8 mg s^{-1}). Of these prey, hammered bivalves were less profitable (4-6 mg s^{-1}) than those which were stabbed (6-8 mg s^{-1}). Taking the ratio shell weight to flesh weight as a measure of the amount of armour, profitability was directly related to prey armour (Fig. 10); clearly, it was least for the most heavily armoured prey.

Figures 2-10 show the time actually taken to handle prey and so ignores the waste handling time spent on rejected prey. If waste handling times due to prey being rejected or stolen prey were included, the graph for the soft-bodied prey in Figs. 8 and 9 would not change much because few prey were refused and waste handling time was very short (Ens *et al.* 1996a). In contrast, waste handling times had a significant effect on prey profitability in armoured prey, such as Mussels hammered on the dorsal or ventral side

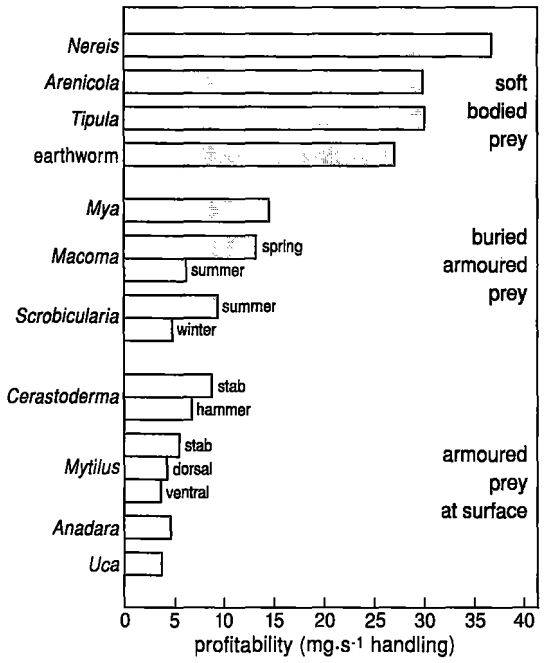

Fig. 9. Comparative profitabilities of different prey species, calculated as a relative deviation from the relationship between profitability and prey weight (Fig. 8, using a common slope but different intercepts for armoured and soft-bodied prey) and then standardized for a prey of 200 mg. According to a one-way analysis of variance, the standardized profitabilities differ significantly between the species and categories concerned ($R^2 = 0.87$, $p < 0.001$, $n = 400$). The values are extrapolations for some small prey always weighing less than 200 mg.

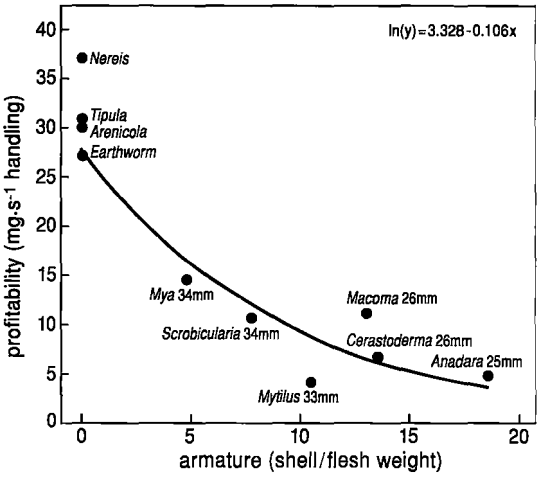

Fig. 10. Profitability as a function of the armour index in prey containing 200 mg flesh. The corresponding shell length of the bivalves is indicated. The fitted curve is highly significant ($r = -0.91$, $p = 0.0003$). Profitability of the different prey species was standardized for a prey of 200 mg (see Fig. 9). Armature index is defined as the ratio shell to flesh weight for the size classes concerned. Shell weights from Wolff *et al.* (1987), Zwarts & Blomert (1992); flesh weights from Zwarts (1991) and Zwarts & Wanink (1993).

(Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996a, Meire 1996c). As a consequence, the difference in profitability between soft-bodied and armoured prey at the surface is even larger than shown.

In conclusion, prey weight varies by a factor of 1000 whereas, over this range, handling time increases only about 100 times. The relationship between handling time and prey weight is different for the various prey species. It takes 4.4 times more time to prepare and consume the flesh of armoured prey compared with a soft-bodied prey of a similar energy value. Among the armoured prey, surface prey take more time to handle than burying species. The handling time of burying prey increases, however, if they are taken from deep beneath the surface.

Intake rate and prey weight

If the time taken to search for prey is negligible, the intake rate during feeding is equal to the prey profitability, the intake rate as the prey is being handled. The profitability of the prey thus sets the upper limit to intake rate. We might therefore expect that the maximum recorded intake rate, and possibly also the average, to increase when Oystercatchers feed on the more profitable prey. As large prey are more profitable than small ones, we would expect an increase of intake rate with the average weight of the prey taken. There was indeed an effect of prey weight on intake rate, but intake rates were always relatively high when the birds foraged less than 1 h after a long resting pe-

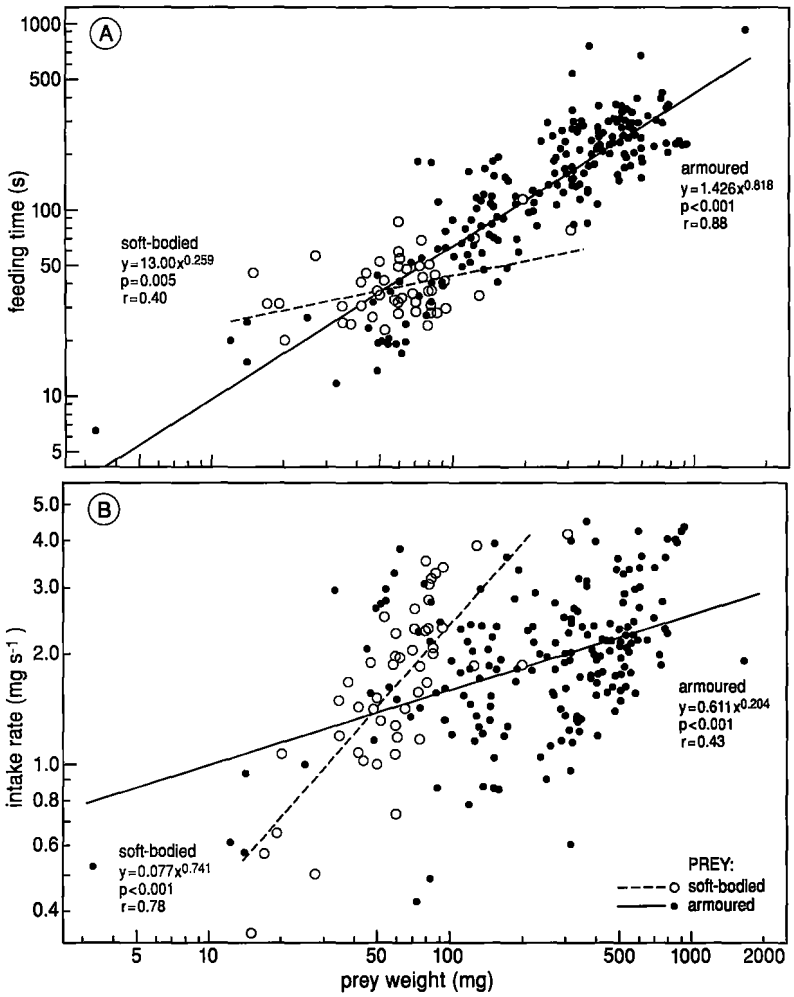

Fig. 11. (A) Feeding time per prey (s) and (B) intake rate (mg s^{-1} feeding) as a function of average prey weight, given separately for soft-bodied and armoured prey species. Sources: *Anadara* (Swennen 1990), *Arenicola* (Bunskoeke 1988), earthworms (Heppleston 1971, Hosper 1978, Ens unpubl.), *Littorina* (Boates & Goss-Custard 1992), *Macoma* (Hulscher 1982 & unpubl., Bunskoeke *et al.* 1996, Hulscher *et al.* 1996), *Mya* (Zwarts & Wanink 1984, Bunskoeke 1988, Hulscher unpubl.), *Patella* (Safriel 1976), *Tipula* (Safriel 1976, Hosper 1978, Zwarts & Blomert 1996, Ens unpubl.), *Uca* (Ens *et al.* 1993); for other species see the legends of Figs. 12-15, or the appendix for a complete list. Feeding time is not given in the appendix, but can be calculated by dividing prey weight by intake rate. Eleven studies for which the feeding time was less than one hour are not included. The two lines in panel (A) differ significantly from each other according to an analysis of variance: $R^2 = 0.814$ for prey weight and $R^2 = 0.011$ for the two groups; the regression lines in panel (B) explain each less variance, but differ more from each other: $R^2 = 0.214$ for prey weight and $R^2 = 0.020$ for the two groups ($n = 240$).

riod. We focus here on intake as a function of prey weight and exclude the eleven studies in which feeding time was less than one hour. We analyse elsewhere the relation between intake rate, feeding activity and duration of the feeding time (Zwarts *et al.* 1996b).

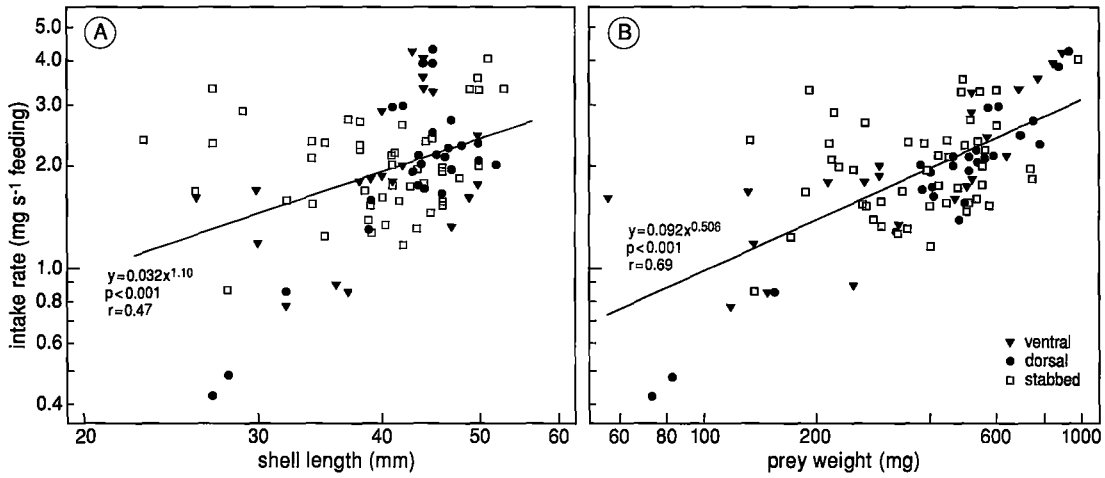

Fig. 12. The intake rate as a function of (A) shell length and (B) average weight of *Mytilus* taken. Sources: Drinnan (1958a), Heppleston (1971), Koene (1978), Zwarts & Drent (1981), Ens & Goss-Custard (1984), Speakman (1984), Meire & Ervynck (1986), Sutherland & Ens (1987), Boates (1988), Cayford & Goss-Custard (1990), Boates & Goss-Custard (1992), Maagaard & Jensen (1994), Ens & Alting (1996b), Ens *et al.* (1996b), Meire (1996b), Goss-Custard (unpubl.), Hulscher (unpubl.), Zwarts (unpubl.).

Most of the prey taken by Oystercatchers weighed between 30 and 1000 mg. Within this range, the average feeding time per prey, the time to find and consume one prey, increased with prey weight, but the rate of increase seemed to differ between soft-bodied and hard-shelled prey (Fig. 11A). The exponent was 0.82 in hard-shelled prey, so clearly sub-proportional, and was only 0.26 in soft-bodied prey. Since the increase in average feeding time with prey weight was less than proportional, the intake rate, being the ratio of prey weight and feeding time per prey, increased with prey weight (Fig. 11B). The increase was more pronounced in soft-bodied prey than in hard-shelled prey for which the variation was very large over the range of 1 to 3 mg s^{-1} within which the majority of the intake rates occurred.

Figures 12 to 15 relate intake rate to the weight and length of the prey, separately for each species. Intake rate increased with prey length in Mussels (Fig. 12A), although the relationship was more pronounced when intake rate was plotted against prey weight (Fig. 12B). Feeding method did not explain a significant part of the variation (prey size: $r = 0.001$, $p = 0.96$, $n = 95$; prey weight: $r = 0.013$, $p = 0.35$, $n = 97$). Prey weight was also a better predictor of intake rate (Fig. 13B) than prey size in cockle-eating Oystercatchers (Fig. 13A). Similarly, intake rate increased with length and weight in *Scrobicularia* (Fig. 14). However, there was no relationship in *Macoma*, probably because the variation in the range of size and weight classes taken was too limited.There were insufficient data for *Mya* (see appendix). In contrast, the increase of intake rate with prey weight was very steep in Ragworms (Fig. 15). Indeed, the increase was proportional, implying that the feeding rate (number of worms taken per unit time feeding) was independent of the average weight of the prey taken. Apparently, Oystercatchers that fed on small Ragworms were not able to compensate for the low prey weight by a higher rate of feeding.

We used multiple regression analysis, with the species as dummy variables, to explore the degree to which the variation around the regression lines in Fig. 11 could be attributed to differences between prey species. In soft-bodied prey, the vari-

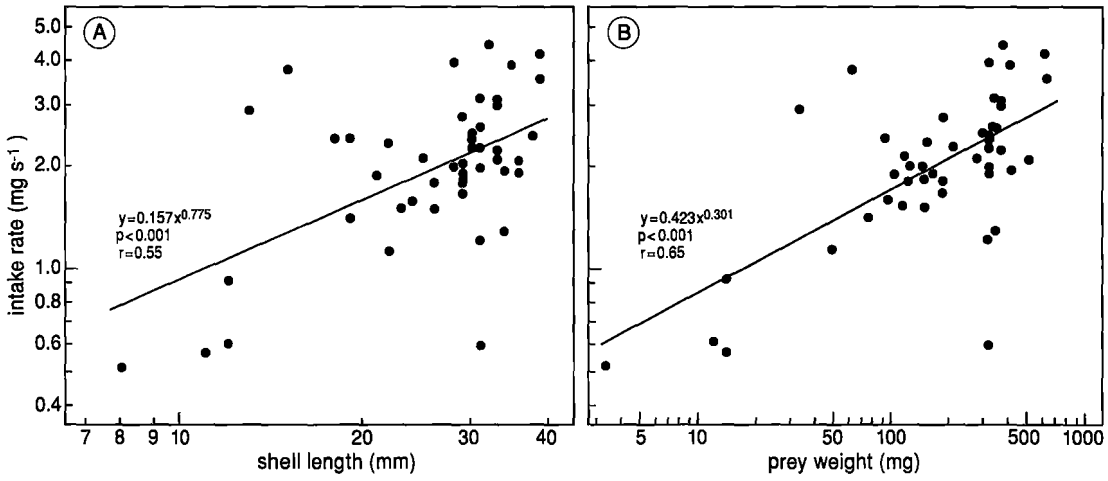

Fig. 13. The intake rate as a function of (A) shell length and (B) average weight of *Cerastoderma* taken. Sources: Drinnan (1957), Davidson (1967), Brown & O'Connor (1974), Hulscher (1976 & unpubl.), Goss-Custard (1977), Sutherland (1982b & c), Leopold *et al.* (1989), Ens *et al.* (1996b & c), Meire (1996b), Exo, Smit & Zwarts (unpubl.).

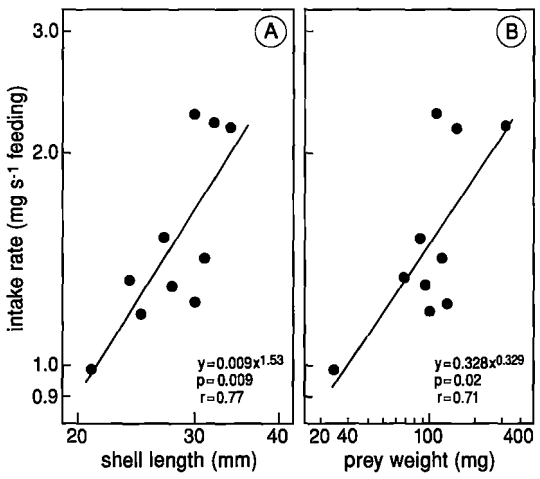

Fig. 14. The intake rate as a function of (A) shell length and (B) average weight of *Scrobicularia* taken. Sources: Blomert *et al.* (1983), Wanink & Zwarts (1985 & 1996), Habekotté (1987), Boates & Goss-Custard (1989), Hulscher *et al.* (unpubl.), Zwarts (unpubl.).

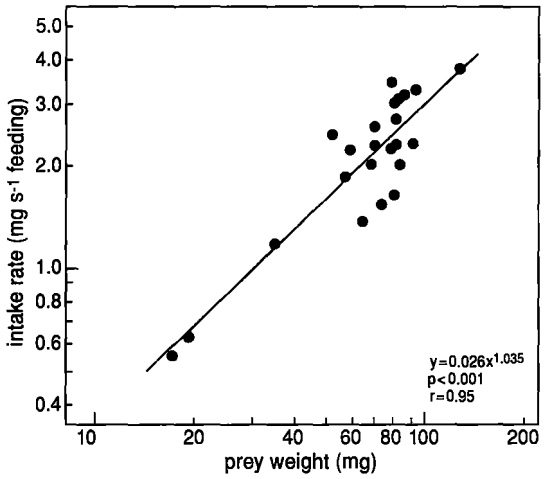

Fig. 15. The intake rate as a function of the average weight of *Nereis* taken. Sources: Boates & Goss-Custard (1989), Triplet (1989), Bunskoeke *et al.* (1996), Durell *et al.* (1996 & unpubl.), Hulscher (unpubl.).

ance explained increased from 60% to 69% if we assumed a similar slope for the species (exponent = 0.656) but different intercepts. By using four parallel slopes, the regression lines became less steep than the one used for all four species species combined (exponent = 0.741). However, using different slopes for the different soft-bodied prey increased the explained variance by less than 1% and has thus not much sense. In the armoured prey species, using parallel slopes for all species

Table 3. Average intake rate (mg $s^{-1} \pm SD$) and prey weight per prey species; *n* is the number of studies (given in appendix). Eleven studies with a feeding period < 1 h and two studies with extremely low intake rates (nrs. 196 & 197 in appendix) have been excluded.

Species	mg s^{-1}	*SD*	mg	*n*
Anadara	1.85		1637	1
Arenicola	2.96	1.64	216	2
Cerastoderma	2.17	0.93	230	48
Earthworms	1.18	0.53	71	5
Littorina	1.24	0.27	138	8
Macoma	2.34	0.59	67	12
Mya	3.14	0.64	172	3
Mytilus ventral	2.04	0.92	418	26
Mytilus dorsal	2.10	0.93	513	27
Mytilus stab	2.05	0.69	409	48
Nereis	2.00	0.95	67	23
Patella	2.35		120	1
Scrobicularia	1.74	0.75	178	11
Tipula	1.34	0.48	53	18
Uca	1.78		786	1
all species	2.00	0.85		240

(exponent = 0.375) added 31% to the 18% of the explained variance that could be attributed to prey weight using the single regression line (exponent = 0.204) in Fig. 11B. On the assumption that all the regression lines for the armoured prey species were not parallel, the explained variance increased again, but only from 49% to 56%. We therefore conclude that (1) in each species, the intake rate increases with prey weight, (2) the rate of increase differed between soft-bodied and armoured prey species, (3) the rate of increase did not differ much among the four soft-bodied and among the twelve armoured prey species, and (4) intake rate differed between the species when prey of similar weight were taken.

Table 3 gives the average intake rate per prey species. According to a one-way analysis of variance, the differences were significant ($R^2 = 0.185$, $p < 0.001$, $n = 240$). The highest intake rate was found in birds feeding on *Mya* or *Arenicola* and the lowest in birds eating earthworms, *Tipula* or *Littorina*. Since intake rate increased with prey weight in each prey species, a similar relationship might be expected between average intake rate and average weight across prey species. There was, however, no such relationship ($r = 0.00$). But in order to rule out any possible effect of prey size on intake rate, the intake rate was standardized to a prey weight of 200 mg, using the predicted values from the multiple regressions with a common slope but different intercepts for the different soft-bodied and armoured prey species. Intake rate averaged for each species now differed more from each other. In conclusion, prey weight determines to a large degree the intake rate, but differences between the prey species are even larger.

Intake rate and prey density

A review of the effect of prey density on intake rate was only attempted for Oystercatchers feeding on Cockles. We selected ten cockle studies, from the twelve available. As discussed by Zwarts *et al.* (1996b) intake rate was presumably overestimated by Goss-Custard (1977), while Triplet (1994a) does not present sufficient details to be included in the analysis.

If birds do not vary their search rate and prey selection with prey density, a type 2 functional response would be expected (Holling 1959). Although the levelling off in the intake rate at high prey density in the experiments of Hulscher (1976) resembled this type of response (redrawn in Fig. 16), the assumptions underlying the model were not met (Wanink & Zwarts 1985). As had already been suggested by Hulscher (1976), the birds increasingly specialized on easy prey with short handling times when prey density increased. Thus, even in a controlled experiment, Holling's functional response equation was too simple to describe the feeding behaviour of Oystercatchers.

The situation in the wild is still more complicated, because changes in prey density are usually accompanied by variation in prey condition and prey size (e.g. Goss-Custard 1977, Sutherland 1982a). Sutherland (1982a & b) compared the feeding behaviour of Oystercatchers visiting twelve plots where the cockle density varied be-

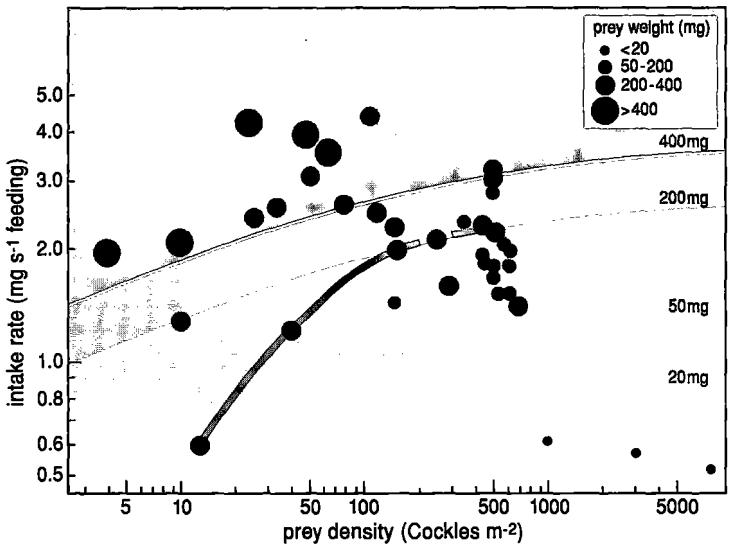

Fig. 16. Intake rate of cockle-feeding Oystercatchers as a function of prey density (n m^{-2}) assembled from ten studies. Hulscher (1976) and Leopold *et al.* (1989) offered caged birds different prey densities. Drinnan (1957), Sutherland (1982a, b & c), Ens *et al.* (1996b & c), Meire (1996b), Exo *et al.* (unpubl.), Hulscher (unpubl.) and Hulsman (unpubl.) observed birds in the wild. All details are given in the appendix. The four curves are based upon the multiple regression equation: $Y = 0.238X_1 - 0.012X^2_1 + 0.476X_2 - 2.727$ ($R^2 = 0.670$, $n = 38$, $p < 0.001$), with Y = ln(*intake rate*), X_1 = ln(*prey density*) and X_2 = ln(*prey weight*). The grey line connects the measured intake rate of a captive Oystercatcher offered Cockles of 313 mg in different densities (Hulscher 1976).

tween 10 and 600 prey m^{-2}. He found a levelling off in the feeding rate at about 9 Cockles min^{-1}. However, the highest intake rate was achieved at low prey densities because prey were large where their density was low: r = -0.90 for ln(*density*) against prey weight. A multiple regression analysis revealed that the intake rate was highly dependent on prey weight ($R^2 = 0.417$, $p = 0.0002$) as well as on prey density ($R^2 = 0.407$, $p = 0.001$). With the exception of the plot with the lowest prey density of 10 Cockles m^{-2}, all these values of intake rate fitted rather well with the general relationship between intake rate and prey weight (Fig. 13).

Intake rate as a function of prey weight and density has also been calculated in a multiple regression of the combined data set for the 38 measurements taken from the ten studies on cockle-feeding birds depicted in Fig. 16. Again, the effect of prey weight was highly significant ($R^2 = 0.577$, $p < 0.001$) as well as prey density ($R^2 = 0.093$, $p = 0.004$), with a highly negative correlation between ln(*density*) and ln(*prey weight*) (r = -0.72). Figure 16 shows the intake rates predicted by the multiple regression analysis as a function of prey density for Cockles weighing 20, 50, 200 and 400 mg. These curves can be compared directly with the 38 measurements, since the prey weight has been indicated by four different symbols. It is obvious that intake rates are well predicted at high prey density but not at low. This may be due to the inevitably larger sampling error when prey density is low. Moreover, there are no studies of birds feeding on small Cockles occurring in low densities. Hence the curves for small Cockles at low prey densities must be considered as extrapolations. The regression analysis may systematically overestimate the intake rate at low prey densities because the samples refer to average density within a plot, whereas the birds would presumably select the richer patches within a plot. This typical problem for field studies was absent in Hulscher's

(1976) experimental study in which Oystercatchers fed in a small plot with homogeneous prey density. As would be predicted, the intake rate at low prey densities in that study is indeed below the prediction of the regression model based on all the studies (Fig. 16).

More detailed data are needed to determine intake rate of Oystercatchers on extremely low densities of Cockles. The general conclusion remains, however, that most of the variation in intake rate depends on the profitability of the average prey taken. The effect of prey density may only become apparent at very low densities.

Seasonal variation in intake rate and consumption at low water

Are Oystercatchers able to attain the same intake rate in winter as in summer, given that the food value of the prey in winter may be reduced as much as 40% below that in summer, whereas the harvestable fraction may be considerably reduced in winter due to the greater burying depth and the reduced surface activity of worms (Zwarts & Wanink 1993)? Although a lower intake rate is to be expected, Oystercatchers have to raise their daily consumption to cover the increased thermoregulation costs when winter temperatures drop below the critical level of 10°C. Hence, to keep their body weight constant, they must raise their intake rate and/or extend their feeding period. Since intake rate is highly correlated with the time spent on the feeding area (Zwarts *et al.* 1996b), we exclude in this analysis the intake rates of breeding birds visiting the feeding areas only during short intervals (< 1 h).

Figure 17 plots the average intake rate, measured in the field, against the season. The data are shown separately for Mussels and all other estuarine prey combined, because Mussels have a very poor condition in May (Dare 1975, Dare & Edwards 1975, Cayford & Goss-Custard 1990, Zwarts & Wanink 1993), whereas all other prey species reach their maximum condition in early summer (Chambers & Milne 1979, Zwarts 1991, Zwarts & Wanink 1993, Ens *et al.* 1996b). For birds feeding on Mussels, intake rate reaches its highest level in late summer. For those taking other prey, the highest rate is in early summer.

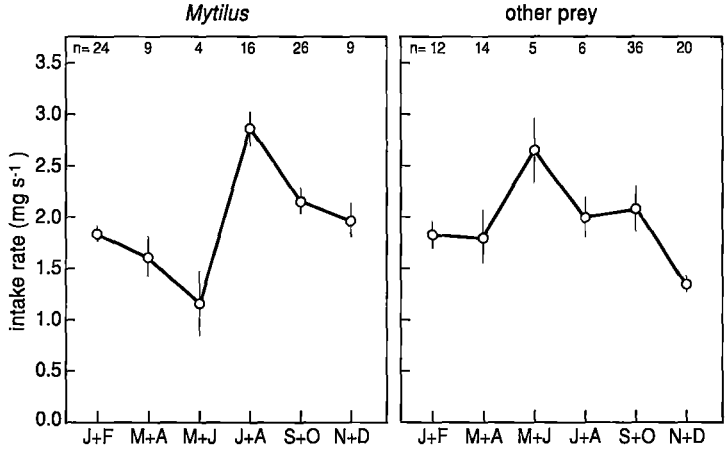

Fig. 17. Seasonal variation in the intake rate (± *SE*) of birds feeding on *Mytilus* (left) or other estuarine prey (right). Excluded are breeding birds, birds feeding for less than one hour, birds feeding in grassland or in Africa, and 13 studies that apparently overestimated intake rate (see Zwarts *et al.* 1996b). The number of studies are shown along the *x*-axis. All sources are given in the appendix. A two-way analysis of variance showed that the intake rate differed significantly between birds feeding on Mussels and the other estuarine prey species, and between the six bimonthly periods ($R^2 = 0.149$, $p = 0.013$, $n = 181$).

Hence, the seasonal trends in intake rate follow the seasonal variation in the prey condition.

This raises the question as to whether there was also a seasonal variation in the total consumption over the low water period in daylight. To remove the effect of variation in exposure time and low water consumption, only those studies in which the available feeding period was 4-6 h were used. With this rather typical exposure time, Oystercatchers consume 24.2 g AFDW (SD = 5.2 g). No significant differences were found, however, in the low water consumption between seasons ($R^2 = 0.20$, $p = 0.06$, $n = 51$; 13 studies that overestimated the consumption (Zwarts *et al.* 1996b) have been excluded). Despite the higher energy demands, consumption during daytime low water periods did not increase in winter. On the other hand, the poorer prey condition had no apparent effect on average low water consumption. This implies that feeding activity must be high in winter, as was shown indeed by Goss-Custard *et al.* (1977) and the studies reviewed here; the average feeding activity is in winter 80-90% compared with 70-80% in summer, although the difference is only weakly significant (R^2 = 0.22, $p = 0.04$, $n = 51$).

In conclusion, the higher intake rate in summer may be attributed to the variation in prey condition, the shallower depth of burying bivalves and the greater activity of the worms. The birds apparently compensate for lower intake rates in winter by feeding for more time during the feeding period. As a consequence, there is no seasonal variation in the amount of food consumed during an average low water period in daylight.

DISCUSSION

Does profitability matter?

Predators cannot choose prey that are not available. For instance, bivalve prey are in any case not available to Oystercatchers if they live out of reach of the bill. Depending on whether bivalves are opened by stabbing or hammering, prey may be defined as available if the bill can be stabbed between the valves, or if the shell is not too strong to hammer a hole in it. Yet, Oystercatchers do not simply take all prey from the available stock. As has been well documented, Oystercatchers refuse small prey due to their low profitability (reviewed by Zwarts *et al.* 1996a). For the same reason, the birds may also select from the available prey only the most profitable prey that are living at a shallow depth (Wanink & Zwarts 1985), that have slightly opened valves (Hulscher 1976, Wanink & Zwarts 1985) and/or that have thin shells (Durell & Goss-Custard 1984, Meire & Ervynck 1986, Sutherland & Ens 1987, Ens & Alting 1996a & b, Meire 1996a & c). Finally, as predicted by the optimal prey choice model (e.g. Krebs & Kacelnik 1991), Oystercatchers are more selective when their intake rate is high (reviewed by Zwarts *et al.* 1996a): as intake rate rises, Oystercatchers successively drop the least profitable prey from their diet. For instance, Oystercatchers take prey from the upper seven cm of the substrate when their intake rate is low but only from the upper three cm when the intake rate is high (Wanink & Zwarts 1985).

What determines prey profitability?

Having firmly established the importance of profitability as a criterion for prey selection in the Oystercatcher, we must enquire in more detail into the factors that determine profitability. The data summarized in Fig. 8 show that the profitability of prey taken by Oystercatchers varies between 1 and 100 mg s^{-1}, i.e. two orders of magnitude! A large part of this variation may be attributed to the way in which prey, through their defenses, are able to prolong the time the predator needs to attack and eat them. For hard-shelled prey, we may hypothesize that the decrease in profitability with the degree of armouring, depicted in Fig. 10, can be explained by the extra time needed to prepare and open the prey. To explore this hypothesis, we must break down the handling time into its consecutive components. First, Oystercatchers must recognize prey as edible. However, it is likely that the time-cost of recognition is so small that it can be safely ig-

nored. For instance, Wanink & Zwarts (1985) found that detection and rejection of prey happened so quickly in Oystercatchers feeding on buried prey that it could not be measured, not even with the aid of a high speed camera. Thus, handling time may be subdivided into three significant components: (1) lifting and preparing time; (2) opening and cutting time and (3) eating time (Speakman 1984, Wanink & Zwarts 1985, 1996). What is known about the relative duration of these components?

(1) Lifting and preparing time When prey located in the substrate are lifted to the surface to be opened, lifting itself takes, on average, a quarter of the total handling time (Wanink & Zwarts 1985, 1996). The handling time is 1.25-1.50 times longer when burrowing prey, such as *Macoma*, *Mya* and *Scrobicularia*, are extracted from the substrate rather than being eaten *in situ* (Wanink & Zwarts 1985, 1996, Hulscher *et al.* 1996; see also Fig. 5). A soft-bodied prey taken from the surface, such as the leatherjacket, is handled at least twice as fast as one which has to be extracted from the substrate. Grasping or lifting time is also zero in Oystercatchers that stab the bill directly between the valves of Mussels and Cockles, or hammer Mussels *in situ* on the dorsal side of the shell. In contrast, the handling times of Mussels hammered on the ventral side are relatively long because the Mussels have to be torn off the bed and turned upside down (Cayford & Goss-Custard 1990; see also Figs. 2 & 3).

(2) Opening and cutting time Armoured prey must be opened by hammering or stabbing, after which the flesh can be separated from the shell. Opening and cutting are absent in prey eaten whole, but it takes about 2/3 of the handling time of bivalves, and even more when prey are hammered. Before lifted bivalves are opened, they are sometimes transported. Oystercatchers may walk for several seconds with their prey to a site with a substrate firm enough to exert the force to break into the shell. This occurs more often when the substrate is soft and Oystercatchers have to walk to a nearby creek, or to a site where the shells of bivalves that have been opened earlier serve as an anvil. Although untested, the part of the handling time involved in transporting the prey must increase if bivalves are taken from soft substrates.

(3) Eating time Finally, the flesh must be mandibulated and swallowed, sometimes after being washed to get rid of the mud clinging to the flesh. Most prey taken by Oystercatchers are swallowed as one large bit of flesh, after which one or two remaining small morsels are taken from the shell. If bivalves contain more than about 1 g AFDW (*Anadara*, large *Mya*), the flesh is taken in more than one large piece, but such large prey are rarely taken. Eating time is 20 to 30% of the total handling time in Oystercatcher eating bivalves. Since 100% of the handling time of soft-bodied prey is spent in eating the prey, one might expect that the average profitability of soft-bodied prey is about four times as large as that of hard-shelled prey, which is indeed close to what has been found (Fig. 9).

Apart from supporting the contention that prey armouring affects prey profitability through its effect on opening time, the review indicates that we may be able to predict the profitability of novel prey from measurements on the prey only, i.e. without observing its consumption by Oystercatchers first. But before we can do this, it is necessary to make a more detailed assessment of the effect of prey size and prey depth on profitability.

Profitability and prey size

Handling time increases with prey size (Figs. 2-7), but the increase in flesh weight is larger, so that large prey are always more profitable (Fig. 8). Why does it take more time to handle large prey? In *Scrobicularia* and *Mya*, it takes more time to lift a larger prey to the surface, to open the shell and to remove the flesh from the shell and to eat it (Wanink & Zwarts 1996). The relative contributions of these three components of handling time are, however, similar for small and large clams. The same was found by Speakman (1984) who studied the handling of Mussels opened by stabbing Oystercatchers. Independently of mussel size, 65% of the handling time is spent in cutting (called 'manipulation time' by Speakman) and

29% in eating the flesh. An increase with prey size in time spent in prey transport was found in stabbing Oystercatchers feeding on Cockles (Exo, Smit & Zwarts unpubl.). Prey of 20-35 mm were eaten *in situ*, but prey 30-40 mm long were taken to a nearby creek, extending the handling time in the latter case by an extra 31 s, on average.

The greater profitability of the larger size classes is reduced if the greater risk of larger prey being stolen and the greater waste handling time are taken into account. First, Cockles are more often refused after they have been stabbed when they are large (Sutherland 1982c, Triplet 1990). Second, Mussels being hammered are often given up and waste handling time increases steeply with size (Meire & Ervynck 1986, Cayford & Goss-Custard 1990, Ens & Alting 1996a, Meire 1996c) Third, Oystercatchers lose prey to dominant conspecifics and to crows and gulls (Zwarts & Drent 1981, Goss-Custard *et al.* 1982, Ens & Goss-Custard 1984, Swennen 1990). We might expect kleptoparasitism to be more common in large prey as the longer handling time gives the parasite more time to attack, while the higher biomass gives a greater benefit (e.g. Ens *et al.* 1990). However, reviewing the literature on Oystercatchers, Ens & Cayford (1996) found evidence for this relationship across prey species, but not within a prey species. Recently, Triplet (1994b) found that large Cockles were more often stolen by gulls than small ones.

Profitability and prey depth

Experiments with Oystercatchers in cages have shown that the handling time of benthic prey increases with burying depth for three reasons (Wanink & Zwarts 1985, Hulscher *et al.* 1996). First, when prey are eaten *in situ*, the eating time is longer when prey live at greater depths. Second, if prey are lifted, the lifting time increases with depth. Third, it always takes more handling time to lift prey to the surface than to eat them *in situ* and deep-living prey are lifted more often than shallow ones. Two lines of evidence suggest that similar relationships hold in the field. First, *Scrobicularia* are handled about twice as fast in summer, when they live at shallow depth, as prey of similar size in winter (Fig. 4A). As prey in summer contain about 1.5 times as much flesh as they do in winter, the profitability of *Scrobicularia* is three times greater in summer than in winter. Similarly, handling time in *Macoma* in August is 1.5 longer than in spring (Fig. 5A), presumably because the prey have to be pulled from greater depths: *Macoma* live closest to the surface in June and July (2 cm) and burrow more deeply from July onwards to reach the greatest depth in December-January (5 cm) (Zwarts & Wanink 1993). Although *Macoma* do remain the entire year within reach of the Oystercatcher's bill, the birds do not feed on them between September and March. If the 50% increase of handling time in August is indeed due to the increased depth of *Macoma*, their greater depth in mid-winter would make *Macoma* a highly unprofitable prey. The profitability of *Macoma* 18 mm long would decrease from 10 mg s^{-1} in mid-summer to 3-4 mg s^{-1} in August and possibly less than 1 mg s^{-1} in mid-winter. Since profitability also decreases due the decline in body condition (Zwarts 1991), an increasing proportion of the medium-sized *Macoma* would be dropped from the diet from June onwards. Hence, only the largest prey are still sufficiently profitable to be taken in August (Bunskoeke *et al.* 1996) and *Macoma* finally disappears from the diet altogether in September (Blomert *et al.* 1983).

Predicting the profitability of new prey

Exotic species are often introduced into ecosystems, either by accident, or on purpose. The effects of such introductions are hard to predict. It would therefore be of great practical value if we could predict the profitability of a prey to a predator before the predator ever ate one. It would also be a good test whether we fully understand the determinants of profitability. In our case, the American razor clam *Ensis directus* is an obvious candidate for prediction. This bivalve did not occur in the Wadden Sea until 1979. It has spread rapidly and now occurs in many places (Swennen *et al.* 1985, Beukema & Dekker 1995). In contrast to related endemic razor clam species, which only

live subtidally, it occurs on intertidal mudflats and therefore constitutes a potential prey to which the Oystercatcher cannot have evolved any special adaptations, yet Oystercatchers have been seen taking *Ensis* by Swennen *et al.* (1985). The birds took *Ensis* 83 mm long, on average, containing 331 mg dry flesh. Since the weight of the shell was 1640 mg, the shell/flesh ratio was 4.95. This is a rather low value for the armouring index, but comparable to *Mya* (Fig. 10). Given the value of this index, we would predict from Fig. 10 that *Ensis* 83 mm long would have a profitability of 15 mg s^{-1} and thus be handled in 22 s. Although Swennen *et al.* (1985) did not measured handling times, they noted that the prey were handled in less time than Cockles of 280 mg occurring in the same area. The handling time of such a Cockle is about 30 s (Fig. 3, Table 1) and thus indeed longer than the predicted 22 s. *Ensis* is a difficult prey to attack since it is highly mobile and buries very rapidly into the substrate when attacked (Schneider 1982, Henderson & Richardson 1994), but if the prey can be pulled out the sand, it is easy to open as the valves gape.

Some dozens of Oystercatchers were recently observed feeding on another razor clam, *Solen marginatus*, in Dakhla Bay and Khniffiss lagoon, S. Morocco (Exo, Smit & Zwarts unpubl.). These birds took prey 4 to 9 cm long that were present just beneath the surface. The clams were handled in 10-20 s. This implies that, as expected, their profitability resembles that of *Mya* and *Ensis*.

Consequences of variation in profitability for intake rate

The intake rate of Oystercatchers usually varies between 1 and 3 mg s^{-1} (Zwarts *et al.* 1996a & b, this paper) and is the mathematical product of three variables: the searching time, the handling time and the prey weight. Since profitability is simply the ratio of prey weight to handling time, intake rate will necessarily increase with profitability if searching time remains constant and with decreasing searching time if profitability remains constant. However, this is difficult to test as our review does not deal with controlled experiments, but with field data gathered in many different localities under many different circumstances. We might from these field data equally suggest that intake rates are more or less constant and vary independently of prey profitability, because the birds will choose not to feed in poor areas with small prey at low densities and interference will depress intake rate in the best feeding areas with high densities (e.g. Zwarts & Drent 1981).

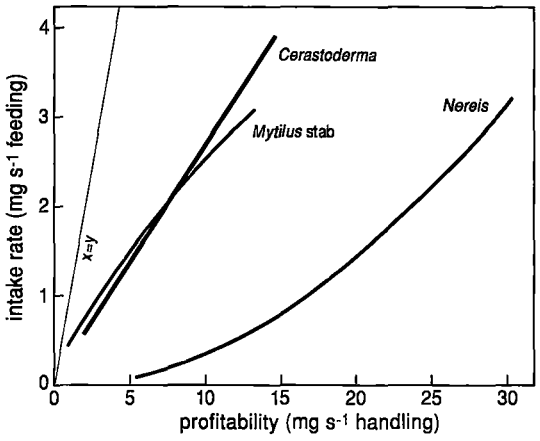

Fig. 18. The intake rate (mg s^{-1} feeding) as a function of profitability (mg s^{-1} handling) were Oystercatchers to feed on *Mytilus*, *Cerastoderma* and *Nereis* of different weights. The graphs are based upon the relationships between profitability and prey weight (Table 1) and between intake rate and prey weight (Figs. 12, 13 & 15). For *Mytilus* a selection is made of birds using the stabbing technique.

Within a prey species, profitability (Figs. 2-7, Table 1) as well as intake rate (Figs. 11-15), increases with prey size. Hence, intake rate increases with profitability (Fig. 18). All else being equal, a doubling of profitability will have little impact on the intake rate when the birds spend most of their time searching, but will nearly double intake rate when the birds spend most of their time handling. It is therefore not surprising that in Fig. 18 profitability differences strongly affect intake rate in Cockles and Mussels, in which handling time is very long, but have much less effect when the birds search for *Nereis*, in which most time is spent in searching.

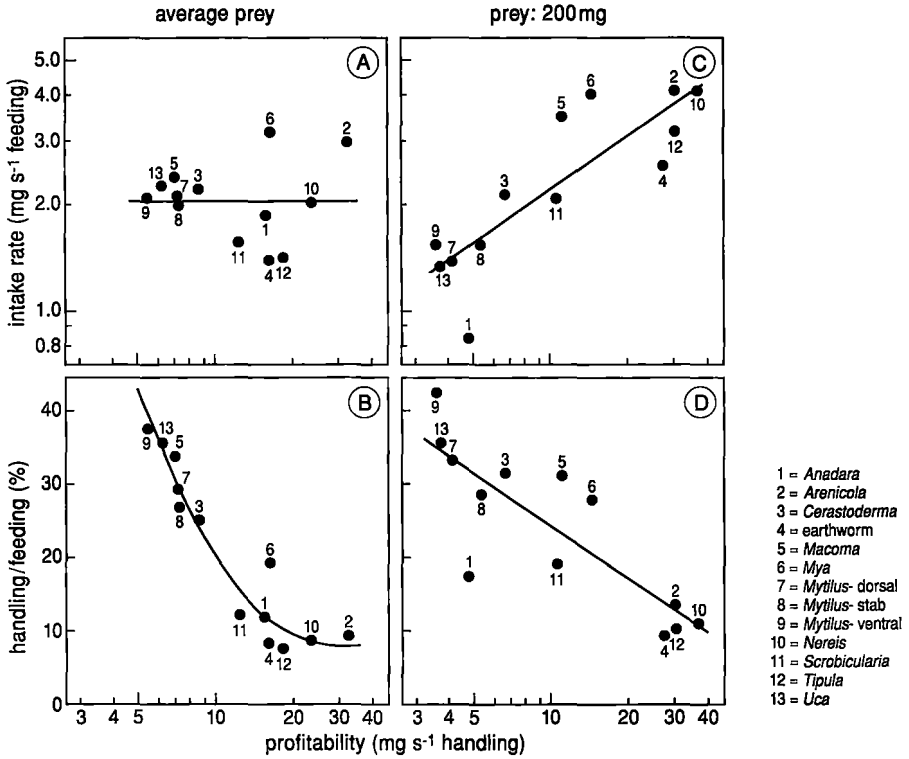

Fig. 19. (A) Intake rate and (B) handling time relative to total feeding time, both averaged per prey species, as a function of the average prey profitability. Per cent handling time, shown in panel (B), was calculated from the averages shown in panel (A). Similar relationships are shown in (C) and (D), with the profitability and intake rate standardized to prey of 200 mg. The standardized profitability of the different prey species was taken from Fig. 9. The intake rate was calculated for prey weighing 200 mg, such as predicted by two multiple regression analyses on the effect of prey weight on the intake rate with soft-bodied or armoured prey species as dummy variables (see text). The values are extrapolations for some small prey always weighing less than 200 mg.

To investigate the relationship between profitability and intake rate between prey species, we plotted the average intake rate per species (Table 3) against the average profitability (Fig. 19A). This comparison shows that, even when profitability increases sixfold, the intake rate remains the same. This implies that when the prey species are compared, the average time spent handling as proportion of total feeding time, i.e. handling and search time combined, decreases with profitability (Fig. 19B). Soft-bodied prey are so profitable that, even when 95% of the feeding time is spent in searching, the intake rate remains at 2 mg s^{-1}. If Oystercatchers were also to search for 95% of the feeding time when they take Mussels, their intake rate would reach the extremely low level of 0.1 mg s^{-1}, and they would starve as shown in the next section.

Since average prey weight differed so much between species, we standardized the profitability and intake rate to prey of similar weight choosing 200 mg (Fig. 9). We calculated the intake rate for each species with the same weight, using the multiple regression equations for soft-bodied and armoured prey with different intercepts but parallel slopes. When prey species with similar body

weight are compared, the intake rate doubles within the range of profitabilities observed (Fig. 19C) and the handling time as proportion of the total feeding time halves (Fig. 19D). Thus, when prey species of similar weight are compared, intake rate strongly depends on the profitability, such as was also found within the species.

Profitability and minimal intake rate

What is the minimal intake rate of food on which Oystercatchers can sustain themselves? Oystercatchers in the wild need at thermoneutrality 36 g a day to keep their body weight constant (Zwarts *et al.* 1996b). If they feed for all the five to six hours per low water period during which the feeding areas are usually exposed, the intake rate must be at least about 1 mg s^{-1}. If it is less than this, they have to collect extra food either on the upper shore during the incoming and receding tides and/or on inland grasslands at high tide. The intake rate on the high shore is low, however (Sutherland 1982b, Ens *et al.* 1996c, Meire 1996b), because the large prey taken by Oystercatchers do not occur there or only at very low densities (e.g. Zwarts *et al.* 1996c) and their condition is often poor (Goss-Custard 1977, Sutherland 1982a). Inland grasslands may provide some compensation, but these opportunities are only available locally. Thus, an intake rate of 1 mg s^{-1} may be considered as a limit below which food consumption will in the long term usually be too low.

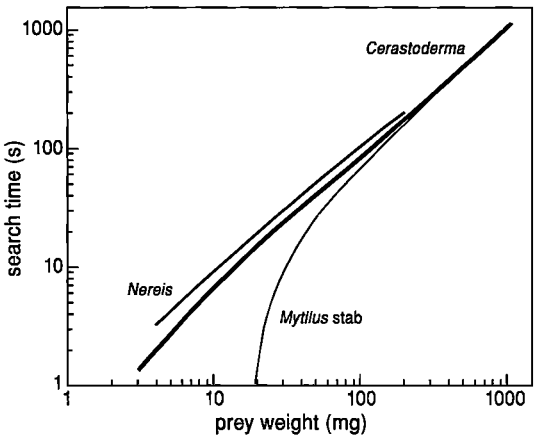

Fig. 20. The time Oystercatchers are allowed to search for prey of a certain weight to achieve an intake rate of 1 mg s^{-1} when they feed on *Mytilus*, *Cerastoderma* and *Nereis*. The searching time is derived from the functions describing the relationship between handling time and prey weight (Table 1). For *Mytilus* a selection is made of birds using the stabbing technique.

If the average weight and handling time of the prey taken are known, it is possible to calculate the length of the searching time at which the intake rate reaches the lower acceptance level of 1 mg s^{-1}. Since the relationships between prey weight and handling time are known (Figs. 2-6, Table 1), we can easily calculate the search time per prey needed to achieve an intake rate of 1 mg s^{-1}. The resulting Fig. 20 shows that if Oystercatchers feed on prey containing more flesh, they may spend much more time in searching to attain a sustainable intake rate. For instance, Cockles > 30 mm long in good condition may contain as much as 1000 mg flesh and are handled in 70 s. Even if the birds have to search for 930 s for each prey, their intake rate is still 1 mg s^{-1}. However, if they feed on cockle spat 8 mm long containing 3 mg flesh, they have to take one prey each 3 s; with a handling time of 1.7 s, the birds cannot search for longer than 1.3 s which requires the spat to be very dense. Cockle spat are indeed found in high densities of many thousands m^{-2} in their first summer. However, although the density of Cockles is usually reduced to about 100 and 10 Cockles per m^2 after one or two winters respectively (Beukema 1982a, Zwarts *et al.* 1996d), Oystercatchers nonetheless achieve a higher intake rate at a low density of these old Cockles than on the high density of spat.

Are there alternative prey for Cockles and Mussels in winter?

Cockles and Mussels are reported as the main prey of the Oystercatchers wintering in NW. Europe (Hulscher 1996). Since Oystercatcher and man compete for the same food resource (e.g. Goss-Custard *et al.* 1996a), it is highly relevant to know to what degree Oystercatchers may switch to other food resources if, for instance due to in-

tensive fishing, few Cockles or Mussels are left. The data summarized in this paper show that, especially in winter, there are only limited possibilities of taking alternative prey.

Burying bivalve species are, on average, more profitable than bivalves living at, or just beneath, the surface (Fig. 9). However, burying bivalve species, such as *Scrobicularia* and *Macoma*, live in winter at twice the depth they do in summer. The increase of handling time with depth makes them, therefore, in winter much less profitable than in summer, by which they become even less profitable than surface-living prey (Fig. 9). Moreover, the search time increases with burying depth (Wanink & Zwarts 1985). Hence, the intake rates would be usually very low were Oystercatchers to feed on *Scrobicularia* an *Macoma* in winter (Zwarts *et al.* 1996d).

In some years, *Mya* is an alternative winter prey, as it does not increase its burying depth during the winter, so many remain accessible all winter. Moreover, this prey is highly profitable, even if taken from deep beneath the surface (Fig. 6). However, only prey of about 20-30 mm are harvestable by Oystercatchers since smaller prey are unprofitable and an increasing proportion of the larger clams burrows out of reach of the Oystercatcher's bill (Zwarts & Wanink 1984). Consequently, Oystercatchers can only feed on *Mya* when they are about 1.5 years old, and since there is no spatfall in most of the years (Beukema 1982b, Beukema *et al.* 1993), Oystercatchers can harvest this food supply only in a minority of the winters (Zwarts *et al.* 1996d).

Two large worm species, *Arenicola* and *Nereis* might provide other alternative source of prey. However, since both species live at great depth, especially in winter (Zwarts & Wanink 1993), Oystercatchers can only feed on them when they come to the surface. Oystercatchers have to wait till Lugworms emerge at the surface to defecate, which means that even actively feeding worms are inaccessible for 99.9% of the time. As Lugworms reduce their feeding activity at lower mud temperatures (Smith 1975, Cadée 1976), they are inaccessible for 100% of the time on many winter days. This is also true for Ragworms which leave their deep burrows to graze at the surface or filter food in the mouth of the burrow. They feed actively on the surface on sunny days in late winter and early spring, but are also inactive on many cold winter days (Esselink & Zwarts 1989, Zwarts & Esselink 1989, Vedel *et al.* 1994).

Another option is to switch to inland grassland areas, where Oystercatchers can feed on earthworms and leatherjackets. The latter prey is still extremely small in winter, and possibly only large enough to feed upon from April to August (Laughin 1967, Blomert & Zwarts unpubl.). Earthworms may be an important prey in winter as long as the fields are not frozen. The 22 studies on the intake rate of Oystercatchers feeding on earthworms and leatherjackets (Heppleston 1971, Hosper 1978, Zwarts & Blomert 1996, Ens unpubl.) all arrive at a rather low intake rate (see appendix). This may explain why grassland is only used as supplemental food resource at high water in winter (Goss-Custard *et al.* 1984), especially after the proceeding low water feeding period was short (Daan & Koene 1981).

What can Oystercatchers do in winter if there are no large Mussels and Cockles? Beukema (1993) describes the exceptional winter of 1990/1991 when this situation occurred in the western part of the Dutch Wadden Sea. The Oystercatchers did not leave the area. The disappearance rate of the alternative prey (small Cockles, *Macoma*, *Mya* and *Arenicola*) was exceptionally high (Beukema 1993), suggesting that the birds started to take prey that they usually ignored and continued to do so, even when the prey density became very low. The intake rate of the Oystercatchers was not measured, but must have been extremely low. Indeed, it may even have been lower than the 0.5 mg s^{-1} observed in the Eastern Scheldt during the autumn of 1986 (Meire 1996b) when the only food source available for Oystercatchers were 0-year Cockles of 8 mm long. Although the winter 1990/1991 was mild, the mortality of Oystercatchers in the Wadden Sea was relatively high (Camphuysen *et al.* 1996). Apparently, the consumption rate in the western Wad-

den Sea was too low to meet their energy requirements, so that part of the birds starved to death.

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SAMENVATTING

Prooisoorten proberen op verschillende manieren aan hun roofvijanden te ontsnappen. In dit artikel wordt een overzicht gegeven hoe de verdediging van de prooi effect heeft op (1) zijn waarde als prooi voor een predator, de Scholekster en (2) de opnamesnelheid van de Scholekster. De prooiwaarde ('profitability') hangt af van vier variabelen. (1) Binnen elke soort leveren grote prooien meer op dan kleine prooien, omdat de toename van vleesinhoud met prooilengte groter is dan de tijd die het kost om die prooien te eten; (2) prooien zonder pantser (wormen en emelten) leveren meer op dan schelpdieren en krabben; (3) schelpdieren die aan het oppervlak voorkomen zijn zwaarder gepantserd dan schelpdieren die ingegraven leven en leveren daarom minder op, zelfs als de schelpen een beetje openstaan en de vogels hun snavel direct naar binnen kunnen steken zonder de schelp open te hakken; (4) bodemprooien leveren minder op als ze dieper zitten ingegraven. Ondanks de grote verschillen in prooiwaarde, verschilt de opnamesnelheid nauwelijks wanneer de prooisoorten worden vergeleken, waarschijnlijk omdat vogels alleen gaan zoeken naar prooien die weinig opleveren als de prooidichtheid heel groot is en de zoektijd per prooi heel kort. Daarentegen neemt de opnamesnelheid binnen de soort toe als prooien meer opleveren. Blijkbaar zijn de vogels niet in staat om de zoektijd te verkorten ter compensatie voor de lagere prooiwaarden. Ofschoon de prooiwaarden per seizoen verschillen als gevolg van de variatie in de prooiconditie, is de variatie in de opnamesnelheid heel klein. Toch is er wel een verschuiving in het dieet. 's Winters worden weinig wormen en ingegraven schelpdieren gegeten en zijn Scholeksters aangewezen op prooien die aan het oppervlak leven.

Appendix

Overview of all studies that measured size and weight of prey taken by Oystercatchers, as well as their intake rate and total consumption in different areas (indicated in last column with a three letter code, but see Fig. 1 for full names and their geographical position in NW. Europe; dak = Baie of Dakhla, S. Morocco and arg = Banc d' Arguin, Mauritania). Size is expressed as prey length (mm), weight as mg AFDW and intake rate as mg AFDW s^{-1} feeding. Column 'Time' gives the time spent on the feeding area (h), 'Feed' the proportion of the time spent feeding while present on the feeding area, 'Cons' the total consumption (g AFDW) during the time spent feeding; 'B' in column 'Br' indicates whether the data concern breeding birds; nm^{-2} gives the prey density (only for Cockles); 'Mus' shows whether Mussels were opened by stabbing (S), ventral hammering (V) or dorsal hammering (D). Column 'Cap' shows whether birds were held in captivity (C); all other studies were done on free-living birds. Column 'Lab' shows whether it was necessary to estimate AFDW from prey volume (V), wet weight (W) or dry weight (D); all other studies measured AFDW; 'F' refers to studies using formaline to store the prey, making a weight correction necessary. For further general explanation see methods, but for details the notes in this appendix. The number of each note corresponds with the number in the first column.

no	species	mm	mg	mgs^{-1}	month	year	time	feed	cons	br	nm^{-2}	mus	cap	lab	sources	area
1	*Anadara*	73	1637	1.85	2	86	7.30	39.4	19.16						Swennen *et al.* 1990	arg
2	*Arenicola*		309	4.12	5/7	86/7				B					Bunskoeke 1988	sch
3	*Arenicola*		124	1.80	8	86									Bunskoeke 1988	sch
4	*Cerastoderma*	22	49	1.13	2	73	8.50	58.8	20.33					D	Brown & O'Connor 1974	str
5	*Cerastoderma*	21	102	1.86	11/3	61/5	8.50	55.0	31.30					W	Davidson 1967	bur
6	*Cerastoderma*	22	154	2.31	1	54	7.50	42.0	26.20		349			V	Drinnan 1957	mor
7	*Cerastoderma*	30	291	2.45	10	54	7.50	50.0	33.08		115			V	Drinnan 1957	mor
8	*Cerastoderma*	12	12	0.61	2	84					1000				Ens *et al.* 1996c	tex
9	*Cerastoderma*	38	316	2.42	2	84									Ens *et al.* 1995c	tex
10	*Cerastoderma*	36	313	1.88	2	84									Ens *et al.* 1996c	tex
11	*Cerastoderma*	12	14	0.93	3	84									Ens *et al.* 1996c	tex
12	*Cerastoderma*	13	33	2.87	4	84									Ens *et al.* 1996c	tex
13	*Cerastoderma*	15	62	3.75	5	84				B					Ens *et al.* 1996c	tex
14	*Cerastoderma*	18	92	2.38	6	84				B					Ens *et al.* 1995c	tex
15	*Cerastoderma*	19	92	2.38	7	84									Ens *et al.* 1996c	tex
16	*Cerastoderma*	34	411	1.91	9	83					4				Ens *et al.* 1995d	tex
17	*Cerastoderma*	36	504	2.05	9	83					10				Ens *et al.* 1995d	tex
18	*Cerastoderma*	39	606	4.19	9	83					23				Ens *et al.* 1995d	tex
19	*Cerastoderma*	31	338	3.09	9	83					49				Ens *et al.* 1995d	tex
20	*Cerastoderma*	39	616	3.54	9	83					64				Ens *et al.* 1995d	tex
21	*Cerastoderma*	31	328	2.57	9	83					79				Ens *et al.* 1995d	tex
22	*Cerastoderma*	32	366	4.45	9	83					107				Ens *et al.* 1995d	tex
23	*Cerastoderma*	11	14	0.57	9	83					3000				Ens *et al.* 1995d	tex
24	*Cerastoderma*	33	274	2.08	1	95	5.00	41.4	15.50		250			F	Exo, Smit, Zwarts unpubl.	dak
25	*Cerastoderma*	28	317	3.94	1	74	5.00	80.3	56.95						Goss-Custard 1977	was
26	*Cerastoderma*	31	313	0.60	7	66					13		C	D	Hulscher 1976	sch
27	*Cerastoderma*	31	313	1.21	7	66					40		C	D	Hulscher 1976	sch
28	*Cerastoderma*	31	313	1.95	7	66					150		C	D	Hulscher 1976	sch
29	*Cerastoderma*	31	313	2.23	7	66	4.00	54.4	17.47		450		C	D	Hulscher 1976	sch
30	*Cerastoderma*	19	76	1.40	8	61	4.76	66.0	15.83		680			V	Hulscher unpubl.	vli
31	*Cerastoderma*	25	117	2.10	10	80	4.50	67.0	22.79		600				Hulscher unpubl.	pae
32	*Cerastoderma*	23	148	1.49	8	78	5.10	63.2	17.29		147				Hulsman unpubl.	pae
33	*Cerastoderma*	33	365	3.05	10	84	2.00				500		C		Leopold *et al.* 1989	tex
34	*Cerastoderma*	33	365	2.97	10	84	3.00				500		C		Leopold *et al.* 1989	tex
35	*Cerastoderma*	33	365	2.19	10	84	5.00				500		C		Leopold *et al.* 1989	tex
36	*Cerastoderma*	29	185	2.74	10	84	2.00				500		C		Leopold *et al.* 1989	tex
37	*Cerastoderma*	29	185	1.64	10	84	3.00				500		C		Leopold *et al.* 1989	tex
38	*Cerastoderma*	29	185	1.77	10	84	5.00				500		C		Leopold *et al.* 1989	tex
39	*Cerastoderma*	8	3.3	0.52	10	87					7600			F	Meire 1996b	oos
40	*Cerastoderma*	34	337	1.28	2	79					10				Sutherland 1982a, b	tra
41	*Cerastoderma*	30	314	2.37	2	79					25				Sutherland 1982a, b	tra

no	species	mm	mg	mgs^{-1}	month	year	time	feed	cons	br	nm^{-2}	mus	cap	lab	sources	area
42	*Cerastoderma*	31	336	2.55	2	79					33				Sutherland 1982a, b	tra
43	*Cerastoderma*	35	403	3.88	2	79					49				Sutherland 1982a, b	tra
44	*Cerastoderma*	30	209	2.25	2	79					145				Sutherland 1982a, b	tra
45	*Cerastoderma*	24	95	1.57	2	79					287				Sutherland 1982a, b	tra
46	*Cerastoderma*	29	162	1.87	2	79					442				Sutherland 1982a, b	tra
47	*Cerastoderma*	29	146	1.80	2	79					450				Sutherland 1982a, b	tra
48	*Cerastoderma*	26	114	1.50	2	79					542				Sutherland 1982a, b	tra
49	*Cerastoderma*	29	143	2.00	2	79					582				Sutherland 1982a, b	tra
50	*Cerastoderma*	28	124	1.97	2	79					598				Sutherland 1982a, b	tra
51	*Cerastoderma*	26	120	1.77	2	79					609				Sutherland 1982a, b	tra
52	Earthworms		38	1.62	5	84				B					Ens unpubl.	tex
53	Earthworms		27	0.49	6	83				B					Ens unpubl.	tex
54	Earthworms		44	1.00	6	84				B					Ens unpubl.	tex
55	Earthworms		50	0.98	12	66									Heppleston 1971	yth
56	Earthworms		197	1.80	4	77	15.00	33.1	32.17					D	Hosper 1978	fri
57	*Littorina*	18	147	1.29	9/3	81/2	6.00	91.8	25.58					D	Boates & Goss-Custard 1992	exe
58	*Littorina*	18	128	1.31	1	81								D	Boates & Goss-Custard 1992	exe
59	*Littorina*	18	127	1.13	2	81								D	Boates & Goss-Custard 1992	exe
60	*Littorina*	18	89	0.85	3	81								D	Boates & Goss-Custard 1992	exe
61	*Littorina*	18	166	1.16	9	81								D	Boates & Goss-Custard 1992	exe
62	*Littorina*	18	150	1.03	10	81								D	Boates & Goss-Custard 1992	exe
63	*Littorina*	18	145	1.40	11	81								D	Boates & Goss-Custard 1992	exe
64	*Littorina*	18	154	1.76	12	81								D	Boates & Goss-Custard 1992	exe
65	*Macoma*		54	2.70	4	86									Bunskoeke *et al* 1996	sch
66	*Macoma*		59	3.20	5	86				B					Bunskoeke *et al* 1996	sch
67	*Macoma*	16	54	2.90	6	86				B					Bunskoeke *et al* 1996	sch
68	*Macoma*	18	79	3.00	7	86									Bunskoeke *et al* 1996	sch
69	*Macoma*	18	45	2.00	8	86									Bunskoeke *et al* 1996	sch
70	*Macoma*		110	1.73	5	84				B					Ens *et al.* 1996d	tex
71	*Macoma*	17	83.1	2.09	5	79	6.07	90.9							Hulscher 1982	pae
72	*Macoma*	17	83.1	2.67	5	79				B					Hulscher 1982	pae
73	*Macoma*	18	74	2.21	6	66	5.50	85.0	37.19	B				D	Hulscher 1982	sch
74	*Macoma*	20	92	2.32	6	66	0.17	100.0	1.42				C	D	Hulscher 1982	sch
75	*Macoma*	18	60	1.47	8	63	4.58	76.5	18.54					V	Hulscher 1982	vli
76	*Macoma*	16	49	2.58	5	81	1.02	76.0	7.20						Hulscher 1982, unpubl.	pae
77	*Macoma*	16	49	3.68	5	81	0.30	75.0	2.98	B					Hulscher 1982, unpubl.	pae
78	*Macoma*	16	64	2.67	6	86	0.50	100.0	4.81				C		Hulscher *et al.* 1996, unpubl.	sch
79	*Macoma*	16	64	3.31	6	86	0.50	100.0	5.96				C		Hulscher *et al.* 1996, unpubl.	sch
80	*Macoma*	15	47	1.51	5	85									Hulscher unpubl.	sch
81	*Mya*		154	3.87	4/8	86/8				B					Bunskoeke 1988	sch
82	*Mya*	40	135	2.91	5	85				B					Hulscher unpubl.	sch
83	*Mya*	36	350	3.00	7	81	0.40	100.0	4.32				C		Wanink & Zwarts 1995	pae
84	*Mya*	28	51	2.65	10	80	5.00	88.0	41.98						Zwarts & Wanink 1984	pae
85	*Mytilus*	39	332	1.27	9/2	81/2	5.25	93.6	22.47			S		D	Boates & Goss-Custard 1992	exe
86	*Mytilus*	39	328	1.27	9/2	81/2	5.25	91.3	21.91			D		D	Boates & Goss-Custard 1992	exe
87	*Mytilus*	36	249	0.89	9/2	81/2	5.25	93.0	15.64			V		D	Boates & Goss-Custard 1992	exe
88	*Mytilus*	40	320	1.12	1	82								D	Boates & Goss-Custard 1992	exe
89	*Mytilus*	39	288	1.13	2	82								D	Boates & Goss-Custard 1992	exe
90	*Mytilus*	35	342	1.20	9	81								D	Boates & Goss-Custard 1992	exe
91	*Mytilus*	34	261	1.09	10	81								D	Boates & Goss-Custard 1992	exe
92	*Mytilus*	39	315	0.95	11	81								D	Boates & Goss-Custard 1992	exe
93	*Mytilus*	38	234	1.03	12	81								D	Boates & Goss-Custard 1992	exe
94	*Mytilus*	43	400	1.89	1	84						D			Cayford & Goss-Custard 1990	exe
95	*Mytilus*	44	379	1.67	1	84						V			Cayford & Goss-Custard 1990	exe
96	*Mytilus*	50	540	2.03	2	84						D			Cayford & Goss-Custard 1990	exe
97	*Mytilus*	50	571	2.37	2	84						V			Cayford & Goss-Custard 1990	exe
98	*Mytilus*	52	461	1.98	3	84						D			Cayford & Goss-Custard 1990	exe
99	*Mytilus*	47	332	1.31	3	84						V			Cayford & Goss-Custard 1990	exe
100	*Mytilus*	37	149	0.85	4	84						V			Cayford & Goss-Custard 1990	exe
101	*Mytilus*	28	83	0.48	4	84						D			Cayford & Goss-Custard 1990	exe

no	species	mm	mg	mgs^{-1}	month	year	time	feed	cons	br	nm^{-2}	mus	cap	lab	sources	area
102	*Mytilus*	27	73	0.42	5	84						D			Cayford & Goss-Custard 1990	exe
103	*Mytilus*	32	118	0.77	5	84						V			Cayford & Goss-Custard 1990	exe
104	*Mytilus*	32	156	0.84	6	84						D			Cayford & Goss-Custard 1990	exe
105	*Mytilus*	44	692	3.30	8	84						V			Cayford & Goss-Custard 1990	exe
106	*Mytilus*	42	610	2.94	8	84						D			Cayford & Goss-Custard 1990	exe
107	*Mytilus*	44	773	3.53	9	84						V			Cayford & Goss-Custard 1990	exe
108	*Mytilus*	45	873	3.90	9	84						D			Cayford & Goss-Custard 1990	exe
109	*Mytilus*	45	931	4.29	10	84						D			Cayford & Goss-Custard 1990	exe
110	*Mytilus*	43	903	4.20	10	84						V			Cayford & Goss-Custard 1990	exe
111	*Mytilus*	44	853	3.93	11	84						V			Cayford & Goss-Custard 1990	exe
112	*Mytilus*	44	872	3.90	11	84						D			Cayford & Goss-Custard 1990	exe
113	*Mytilus*	38	216	1.76	3	56	9.00	75.0	42.77			V		V	Drinnan 1958a	con
114	*Mytilus*	26	56	1.58	12	55	7.00	85.6	34.08			V		V	Drinnan 1958a	con
115	*Mytilus*	45	697	2.41	10	80	3.89	66.5	22.44			D			Ens & Goss-Custard 1984	exe
116	*Mytilus*	42	606	2.59	10	80	3.60	89.5	30.04			S			Ens & Goss-Custard 1984	exe
117	*Mytilus*	38	498	2.25	10	80	4.44	54.2	19.49			S			Ens & Goss-Custard 1984	exe
118	*Mytilus*	41	570	2.91	10	80	3.89	81.0	33.01			D			Ens & Goss-Custard 1984	exe
119	*Mytilus*	39	522	1.80	10	80	3.61	87.2	20.40			V			Ens & Goss-Custard 1984	exe
120	*Mytilus*	40	533	1.58	10	80	4.00	91.2	20.75			S			Ens & Goss-Custard 1984	exe
121	*Mytilus*	39	505	1.55	10	80	4.00	90.9	20.29			D			Ens & Goss-Custard 1984	exe
122	*Mytilus*	41	551	1.73	10	80	4.03	90.6	22.74			S			Ens & Goss-Custard 1984	exe
123	*Mytilus*	47	749	2.67	10	80	4.33	56.4	23.47			D			Ens & Goss-Custard 1984	exe
124	*Mytilus*	41	551	1.98	10	80	4.00	94.0	26.80			S			Ens & Goss-Custard 1984	exe
125	*Mytilus*	38	271	2.64	7	83						S			Ens *et al.* 1996a	sch
126	*Mytilus*	45	520	3.22	7	83						V			Ens *et al.* 1996a	sch
127	*Mytilus*	35	390	2.30	2	84						S			Ens *et al.* 1996c	tex
128	*Mytilus*	34	351	2.31	3	84						S			Ens *et al.* 1996c	tex
129	*Mytilus*	27	191	3.28	4	84						S			Ens *et al.* 1996c	tex
130	*Mytilus*	29	224	2.84	5	84				B		S			Ens *et al.* 1996c	tex
131	*Mytilus*	23	134	2.33	6	84				B		S			Ens *et al.* 1996c	tex
132	*Mytilus*	27	217	2.30	7	84						S			Ens *et al.* 1996c	tex
133	*Mytilus*	37	518	2.68	7	83						S			Ens *et al.* 1996d	tex
134	*Mytilus*	44	380	1.69	1	82						D			Goss-Custard unpubl.	exe
135	*Mytilus*	40	300	1.33	1	82						S			Goss-Custard unpubl.	exe
136	*Mytilus*	47	509	1.91	1	83	4.68	89.4	28.77			D			Goss-Custard unpubl.	exe
137	*Mytilus*	49	469	1.58	1	94						V			Goss-Custard unpubl.	exe
138	*Mytilus*	43	404	1.72	2	83	4.68	90.0	26.08			D			Goss-Custard unpubl.	exe
139	*Mytilus*	44	425	1.73	2	83	4.68	100.0	29.15			S			Goss-Custard unpubl.	exe
140	*Mytilus*	50	502	1.71	2	94						V			Goss-Custard unpubl.	exe
141	*Mytilus*	39	285	1.38	3	82						S			Goss-Custard unpubl.	exe
142	*Mytilus*	44	379	1.99	3	82						D			Goss-Custard unpubl.	exe
143	*Mytilus*	43	350	1.29	3	83						S			Goss-Custard unpubl.	exe
144	*Mytilus*	46	408	1.62	3	83						D			Goss-Custard unpubl.	exe
145	*Mytilus*	42	444	1.55	9	83	4.68	99.0	25.85			S			Goss-Custard unpubl.	exe
146	*Mytilus*	44	538	2.31	9	83	4.68	85.7	33.35			S			Goss-Custard unpubl.	exe
147	*Mytilus*	43	481	1.70	9	83	4.68	94.2	26.98			S			Goss-Custard unpubl.	exe
148	*Mytilus*		480	1.36	9/10	81						D			Goss-Custard unpubl.	exe
149	*Mytilus*		400	1.50	9/10	81						S			Goss-Custard unpubl.	exe
150	*Mytilus*	45	504	1.45	10	82	4.68	91.3	22.30			S			Goss-Custard unpubl.	exe
151	*Mytilus*	46	559	2.08	10	82	4.68	81.3	28.49			D			Goss-Custard unpubl.	exe
152	*Mytilus*	48	748	1.81	11	81	4.95	92.5	29.84			S			Goss-Custard unpubl.	exe
153	*Mytilus*	41	424	2.12	11	81						S			Goss-Custard unpubl.	exe
154	*Mytilus*	50	779	2.27	11	81	4.95	82.5	33.37			D			Goss-Custard unpubl.	exe
155	*Mytilus*	44	461	2.10	11	81						D			Goss-Custard unpubl.	exe
156	*Mytilus*	47	530	2.19	11	82	4.68	80.6	29.74			D			Goss-Custard unpubl.	exe
157	*Mytilus*	46	503	1.54	11	82	4.68	91.6	23.77			S			Goss-Custard unpubl.	exe
158	*Mytilus*	39	340	1.67	12	81						S			Goss-Custard unpubl.	exe
159	*Mytilus*	43	394	1.93	12	82	4.68	94.6	30.76			S			Goss-Custard unpubl.	exe
160	*Mytilus*	45	513	2.10	12	83	4.68	84.6	29.93			D			Goss-Custard unpubl.	exe
161	*Mytilus*	42	404	1.17	12	83	4.68	94.6	18.65			S			Goss-Custard unpubl.	exe

no	species	mm	mg	mgs^{-1}	month	year	time	feed	cons	br	nm^{-2}	mus	cap	lab	sources	area
162	*Mytilus*	45	647	2.11	12	84	4.68	84.6	30.07			V			Goss-Custard unpubl.	exe
163	*Mytilus*	45	591	2.12	12	84	4.68	84.6	30.22			D			Goss-Custard unpubl.	exe
164	*Mytilus*	30	132	1.66	10	66	11.20	80.9	54.15			V		D	Heppleston 1971	yth
165	*Mytilus*	30	136	1.18	12	66	8.90	94.5	35.73			V		D	Heppleston 1971	yth
166	*Mytilus*	34	220	2.07	10	80	6.00	66.4	29.69			S			Hulscher unpubl.	pae
167	*Mytilus*			16.00			0.22	100.0	12.48				C		Hulscher unpubl.	sch
168	*Mytilus*	46	580	1.52	3	77	4.70	65.5	16.85			S			Koene 1978	tex
169	*Mytilus*	46	740	1.94	10	76	4.68	65.5	21.41			S			Koene 1978	tex
170	*Mytilus*	46	251	1.92	3	92	5.00	78.8	27.23			S			Maagaard & Jensen 1994	ska
171	*Mytilus*	45	448	2.35	9	92	4.00	83.6	28.29			S			Maagaard & Jensen 1994	ska
172	*Mytilus*			1.60	10	86	4.08	74.0	17.39			V		F	Meire 1996b	oos
173	*Mytilus*			1.67	10	86	4.12	92.0	22.79			V		F	Meire 1996b	oos
174	*Mytilus*	39	270	1.50	10	86						S		F	Meire 1996b	oos
175	*Mytilus*			1.94	10	86	4.57	52.0	16.60			V		F	Meire 1996b	oos
176	*Mytilus*	41	450	2.10	10	86						S		F	Meire 1996b	oos
177	*Mytilus*	35	172	1.24	10	86						S		F	Meire 1996b	oos
178	*Mytilus*	40	296	1.84	10	86						V		F	Meire 1996b	oos
179	*Mytilus*	41	270	1.77	10	86						V		F	Meire 1996b	oos
180	*Mytilus*	42	297	1.95	10	86						V		F	Meire 1996b	oos
181	*Mytilus*	40	524	2.82	9	82						V		F	Meire & Ervynck 1986	oos
182	*Mytilus*	50	230	1.95	9/4	81						S			Speakman 1984	for
183	*Mytilus*	51	785	4.02	9	73	5.90	76.3	65.15			S			Zwarts & Drent 1981	sch
184	*Mytilus*	53	604	3.30	5	74	1.38	88.0	14.43	B		S			Zwarts & Drent 1981	sch
185	*Mytilus*	50	545	3.27	5	75	1.38	90.2	14.65	B		S			Zwarts & Drent 1981	sch
186	*Mytilus*	50	492	3.53	5	76	1.38	87.4	15.33	B		S			Zwarts & Drent 1981	sch
187	*Mytilus*	49	487	3.27	5	77	1.38	85.3	13.86	B		S			Zwarts & Drent 1981	sch
188	*Mytilus*	26	186	1.65	5	78	1.38	88.9	7.29	B		S			Zwarts & Drent 1981	sch
189	*Mytilus*	38	614	2.19	5	78	5.00	76.4	30.12			S	C		Zwarts & Drent 1981	sch
190	*Mytilus*	32	299	1.56	5	78	5.00	76.4	21.45			S	C		Zwarts & Drent 1981	sch
191	*Mytilus*	34	264	1.52	9	78	6.00	79.0	25.94			S			Zwarts & Drent 1981	sch
192	*Mytilus*	28	137	0.86	3	79	6.00	84.1	15.62			S			Zwarts unpubl.	pae
193	*Nereis*		17	0.56	8/11	81	7.00	96.1	13.56						Boates & Goss-Custard 1989	exe
194	*Nereis*		35	1.17	8	81									Boates & Goss-Custard 1989	exe
195	*Nereis*		19	0.63	9	81									Boates & Goss-Custard 1989	exe
196	*Nereis*		9	(0.13)	10	81									Boates & Goss-Custard 1989	exe
197	*Nereis*		5	(0.19)	11	81									Boates & Goss-Custard 1989	exe
198	*Nereis*		93	2.30	4	86									Bunskoeke *et al.* 1996	sch
199	*Nereis*		84	3.10	5	86				B					Bunskoeke *et al.* 1996	sch
200	*Nereis*		94	3.30	6	86				B					Bunskoeke *et al.* 1996	sch
201	*Nereis*		82	3.00	7	86									Bunskoeke *et al.* 1996	sch
202	*Nereis*		69	2.00	8	86									Bunskoeke *et al.* 1996	sch
203	*Nereis*		81	1.63	8	84	6.83	100.0	40.08						Durell *et al.* 1996, unpubl.	exe
204	*Nereis*		80	2.25	8	84	6.25	92.8	46.98						Durell *et al.* 1996, unpubl.	exe
205	*Nereis*		58	1.82	9	82									Durell *et al.* 1996, unpubl.	exe
206	*Nereis*		71	2.56	9	82									Durell *et al.* 1996, unpubl.	exe
207	*Nereis*		80	3.46	9	83	6.25	93.4	72.71						Durell *et al.* 1996, unpubl.	exe
208	*Nereis*		87	3.18	9	83	6.83	100.0	78.19						Durell *et al.* 1996, unpubl.	exe
209	*Nereis*		82	2.71	9	84	6.83	99.4	66.23						Durell *et al.* 1996, unpubl.	exe
210	*Nereis*		53	2.44	10	82									Durell *et al.* 1996, unpubl.	exe
211	*Nereis*		60	2.21	10	82									Durell *et al.* 1996, unpubl.	exe
212	*Nereis*		71	2.27	10	83	6.25	100.0	51.08						Durell *et al.* 1996, unpubl.	exe
213	*Nereis*		82	2.27	10	83	6.83	100.0	55.81						Durell *et al.* 1996, unpubl.	exe
214	*Nereis*		85	2.00	10	84	6.25	96.3	43.34						Durell *et al.* 1996, unpubl.	exe
215	*Nereis*		129	3.82	7	83									Ens *et al.* 1996d	tex
216	*Nereis*		65	1.38	5	85				B					Hulscher unpubl.	sch
217	*Nereis*		74	1.53	12	84									Triplet 1989	som
218	*Patella*		96	2.35	5/7	65/6								D	Safriel 1976	sko
219	*Scrobicularia*	32	310	2.20	7	79	4.58	70.0	25.39						Blomert *et al.* 1983	pae
220	*Scrobicularia*	30	132	1.22	10/3	81/2	7.00	98.4	30.25						Boates & Goss-Custard 1989	exe
221	*Scrobicularia*	31	121	1.42	1	82								D	Boates & Goss-Custard 1989	exe

no	species	mm	mg	mgs^{-1}	month	year	time	feed	cons	br	nm^{-2}	mus	cap	lab	sources	area
222	*Scrobicularia*	34	149	2.17	2	82								D	Boates & Goss-Custard 1989	exe
223	*Scrobicularia*	30	110	2.27	3	82								D	Boates & Goss-Custard 1989	exe
224	*Scrobicularia*	25	101	1.18	10	81								D	Boates & Goss-Custard 1989	exe
225	*Scrobicularia*	27	89	1.51	11	81								D	Boates & Goss-Custard 1989	exe
226	*Scrobicularia*	24	68	1.32	12	81								D	Boates & Goss-Custard 1989	exe
227	*Scrobicularia*	21	25	0.98	3	84	7.00	80.0	19.76						Habekotté 1987	sch
228	*Scrobicularia*	39	303	4.43	10	81	0.46	100.0	7.34				C		Hulscher *et al.* unpubl.	pae
229	*Scrobicularia*	39	303	8.06	10	81	0.25	100.0	7.25				C		Hulscher *et al.* unpubl.	pae
230	*Scrobicularia*	39	303	9.99	10	81	0.20	100.0	7.19				C		Hulscher *et al.* unpubl.	pae
231	*Scrobicularia*	35	300	3.00	7	81	0.40	100.0	4.32				C		Wanink & Zwarts 1996	pae
232	*Scrobicularia*	36	274	3.40	8	81	0.40	100.0	4.90				C		Wanink & Zwarts 1985	pae
233	*Scrobicularia*	28	94	1.29	4	79	5.50	89.1	22.76						Zwarts unpubl.	pae
234	*Scrobicularia*	29	169	3.55	5	79									Zwarts unpubl.	pae
235	*Tipula*		50	1.47	7	91									Blomert & Zwarts unpubl.	fri
236	*Tipula*		49	1.37	8	93									Blomert & Zwarts unpubl.	fri
237	*Tipula*		60	1.24	4	84									Ens unpubl.	tex
238	*Tipula*		60	1.92	5	84				B					Ens unpubl.	tex
239	*Tipula*		75	1.14	6	83				B					Ens unpubl.	tex
240	*Tipula*		60	1.04	6	84				B					Ens unpubl.	tex
241	*Tipula*		60	0.72	7	84									Ens unpubl.	tex
242	*Tipula*		76	1.80	4	78	14.00	35.7	32.39					D	Hosper 1978	fri
243	*Tipula*		62	1.89	5	77				B				D	Hosper 1978	fri
244	*Tipula*		47	1.84	5	78	17.00	22.0	24.77	B				D	Hosper 1978	fri
245	*Tipula*		42	1.05	6	77				B				D	Hosper 1978	fri
246	*Tipula*		61	1.15	6	78				B				D	Hosper 1978	fri
247	*Tipula*		85	1.95	7	78								D	Hosper 1978	fri
248	*Tipula*		42	1.40	5/7	65/6								D	Safriel 1976	sko
249	*Tipula*		15	0.34	3	77	13.00	59.1	9.40						Veenstra 1978	fri
250	*Tipula*		20	1.04	4	95	14.70	57.3	31.54						Zwarts & Blomert 1996	fri
251	*Tipula*		35	1.45	5	91		39.9		B					Zwarts & Blomert 1996	fri
252	*Tipula*		52	1.28	5	91									Zwarts & Blomert 1996	tex
253	*Uca*		786	2.23	9	88									Ens *et al.* 1993	arg

Notes to appendix

1: AFDW of *Anadara* taken was 3300 mg, but 56% of the prey could not be eaten completely, due to kleptoparasitism by other bird species. Since Swennen estimated that in these cases, on average, 10% of the flesh was eaten, the weight of the average prey taken was estimated to be 1637 mg.

2-3: Since the birds also took *Macoma* and *Nereis*, a selection was made of 5 min periods during which *Arenicola* was the dominant prey.

4: Cockle height has been converted to length using Table 5 in Zwarts (1991); ash assumed to be 20% (being the average winter level; Zwarts 1991).

5: The intake rate varied between 1.4 and 2.2 mg s^{-1} during six different winter months. The data were pooled since the observation times were limited.

8-15: Since the birds also took *Mytilus*, a selection was made of 5 min periods with *Cerastoderma* as dominant prey.

25: Feeding area was exposed 5 h during daylight in January; this is equivalent to 6.5 h per low water period. Goss-Custard (1977) noted that the avarage prey weight was overestimated since small prey were probably missed and flesh also remained in the shell.

26-29: Ash assumed to be 13% in summer (being the average summer value; Zwarts 1991).

31: The flesh remaining in the shell has been measured (14.8% relative to total AFDW).

33-38: The same data are given separately for individuals by Swennen *et al.* (1989).

52-54: Since the birds also took *Tipula*, a selection was made of 5 min periods during which earthworms were the dominant prey.

55: It is assumed that the birds took the average prey present.

56: It is assumed that the ash content is 40% (data for the same area in later years; Blomert & Zwarts unpubl.).

57-64: Ash of *Littorina* in winter is assumed to be 10% (Chambers & Milne 1979).

65-69: Since the birds also took *Nereis*, a selection

was made of 5 min periods during which *Macoma* was the dominant prey.

70: Since the birds also took *Cerastoderma*, a selection was made of 5 min periods during which *Macoma* was the dominant prey.

71-72: The estimation of the consumption per low water feeding period is based upon measurements of the feeding rate in colour-marked non-breeding birds (study 71) and breeding birds (study 72), but the feeding activity and mean prey weight were based on counts and prey collection, respectively, in which breeding and non-breeding birds could not be distinguished. That is why a calculation of the low tide consumption (41 g AFDW) would be too high for the non-breeding birds, even if they remained 6 h on the feeding area, since presumably their feeding activity would be lower than for the breeding birds.

74: Intake rate of captive birds averaged for two experimental conditions (erased and non-erased surface).

76-77: A pair of individually marked Oystercatchers visited tidal mudflats adjacent to their nest during short feeding bouts; studies 76 and 77 give the average for the week before and after eggs were laid, respectively; feeding rate already given by Hulscher (1982: Fig. 29).

81: Since the birds also took *Macoma*, a selection was made of 5 min periods during which *Nereis* was the dominant prey.

82: The birds usually only took the siphon. This partial consumption did not cause an overestimation of the consumption, since the flesh taken was estimated from the size of the pieces of flesh extracted from the shell.

83: The birds took small *Mya* in one jerk, taking the siphon but leaving a part of the body behind in the shell. When this was imitated in the laboratory 22% of the flesh remained behind. This was taken as a correction factor.

85-87: Study 85-87 give same data as study 88-93 averaged for all months and split up for stabbers, dorsal and ventral hammerers. Intake rates are given by Boates (1988). Exposure time according to Goss-Custard (unpubl.).

94-112: Details in Cayford (1988)

115-124: Summaries of the data are published by Ens (1982), Ens & Goss-Custard (1984), Sutherland & Ens (1987).

127-132: Since the birds also took *Cerastoderma*, a selection was made of 5 min periods with *Mytilus* as dominant prey.

134-163: The majority of the data are given in Goss-Custard *et al.* 1984, Goss-Custard & Durell 1987 & 1988. The intake rates were recalculated, however, from the actual AFDW/mussel length relationships measured on the mussel bed, month and year in question, whereas the original paper gave standardized intake rates.

164-165: Ash assumed to be 20% in winter. Observations were restricted to 5 h around low water, and give according to Heppleston (1971) an overestimation when extrapolated to the extreme long exposure times in October (study 164), when the birds were less active at the end of the feeding period.

167: Hungry, captive Oystercatchers were offered shelled *Mytilus*.

182: The flesh remaining in the shell has been measured (7.6% relative to total AFDW).

183-191: The intake rates deviate from those orginally published (Zwarts & Drent 1981), due to recalculation. Exposure time of the mussel bed in May was, as in the other months, 6-6.5 h, but the watched adults were breeding birds and visited the mussel bed during bouts of 83 min, on average, only.

193-197: AFDW is assumed to be 81% of DW (Zwarts unpubl.). Exposure time according to Goss-Custard (unpubl.).

198-202: Since the birds also took *Macoma*, a selection was made of 5 min periods during which *Nereis* was the dominant prey.

203-214: Intake rates of adult and juveniles are pooled.

217: Intake rates pooled over adults and immatures and over three winter periods.

218: AFDW assumed to be 80% of DW.

220-226: AFDW assumed to be 83% of DW (Zwarts 1991). Exposure time according to Goss-Custard (unpubl.).

228-230: Three birds were allowed to take 24 prey each in different sessions with a prey density > 200 prey m^{-2}.

231-232: Intake rate averaged for the experimental sessions with prey density ≥ 100 m^{-2}.

237-241: Since birds also took earthworms, a selection was made of 5 min intervals during which leatherjackets were the dominant prey.

242-247: The diet consisted not solely of *Tipula*, since sometimes large earthworms were also taken, especially in April and July. The ash content of leatherjackets and earthworms was assumed to be 21% and 40%, respectively (data of the same area in later years; Blomert & Zwarts unpubl.). The feeding activity and consumption refer to the day-light period.

248: AFDW assumed to be 79% of DW (Blomert & Zwarts unpubl.).

249: Birds fed from sunrise to sunset. The feeding activity according to the activity counts was 59.1% (but the observed birds fed 83.5% of the time). Weight of the leatherjackets taken was not measured, but assumed to be 15 mg AFDW, being the average weight of prey collected in the same area and the same month in later years (Blomert & Zwarts unpubl.).

253: Ens *et al.* (1993) give feeding rate and size selection. Collection of prey remnants showed, however, that prey size was underestimated (Ens unpubl.). Intake rate was calculated on the basis of corrected size selection. The birds opened the carapace to remove the flesh from it; by not eating the pincers and legs, they ignored 50% of the flesh (Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Not all flesh was eaten from the carapace, since other wader species took flesh from it after Oystercatchers had finished. Whimbrels *Numenius phaeopus* opening *Uca* of similar size left behind 100 mg in the carapace (Zwarts & Dirksen 1990); it is assumed this was the same for Oystercatchers.